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**SPATIAL DYNAMICS AND COMMUNITY STRUCTURE IN
CORAL REEF FISHES (FAMILY LABRIDAE)**

by
Katherine Martha May Jones

A Dissertation
Submitted to the Faculty of Graduate Studies and Research
through the Department of Biological Sciences
in Partial Fulfillment of the Requirements for
the Degree of Doctor of Philosophy at the
University of Windsor

Windsor, Ontario, Canada

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ABSTRACT

This dissertation represents a comprehensive investigation into the behaviours, social interactions, microhabitat use, and spatial dynamics of six ecologically and morphologically similar Caribbean labrid species. The following species were included: *Halichoeres bivittatus*, *H. garnoti*, *H. maculipinna*, *H. poeyi*, *H. radiatus*, and *Thalassoma bifasciatum*. The first study (Chapter II) examined the relationship between fish size and home range area and found a strong, positive relationship for all species. It was also observed that within their individual home ranges, labrids concentrate their activities in core use areas. The second study (Chapter III) investigated behavioural similarities among these species and their life stages. These labrids showed a high degree of overlap in their behaviours. There was a remarkable similarity in ontogenetic changes in these behaviours among the species. As these labrids grow, they spend more time swimming alone, and less time hovering and searching for food. The third study (Chapter IV) investigated the distribution of behaviours and species interactions within home ranges. Some behaviours were randomly distributed throughout home ranges whereas others were non-randomly distributed. On average, individual fish of all species showed higher frequencies than expected of agonistic interactions with damselfish in the peripheral region of their home ranges. This suggested a large influence of the position of damselfish on labrid spatial arrangements. The fourth study (Chapter V) examined microhabitat use. There was a high degree of variability in microhabitat use among individuals within a species. However, all species showed increasing preference for less topographically complex microhabitats as they grow. The fifth study (Chapter VI) was a

manipulative field experiment that demonstrated a mechanistic influence of territorial pomacentrids on space use in one labrid species, *H. bivittatus*. These individuals relocated their home ranges after beaugregory damselfish, *Stegastes leucostictus*, were introduced into their core use areas. In the final study (Chapter VII), the effects of environmental factors on labrid assemblage structure were explored. It was found that zonation is a primary factor affecting labrid assemblage structure. On the back reef, several species were negatively associated with adult beaugregory damselfish. Statistical analyses revealed associations between some labrids and microhabitats that were consistent with observations of microhabitat selectivity within individual home ranges.

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CHAPTER I

GENERAL INTRODUCTION

Coral reef fish, with few exceptions, begin life with a pelagic larval stage and then become rather sedentary once they settle to the reef habitat (Leis 1991, Sale et al. 1994). There is continued interest among coral reef fish ecologists in evaluating the importance of post-settlement processes in structuring adult fish assemblages, e.g. predation (Huntsman 1979, Bohnsack 1982, Hixon 1991, Carr and Hixon 1995), ontogenetic habitat shifts (Lirman 1994, Eggleston 1995), habitat associations (Connell and Jones 1991, Wellington 1992, Booth and Beretta 1994), and competition (Shulman 1985, Robertson and Gaines 1986, Jones 1987, Forrester 1990, 1995, Tupper and Hunte 1994). This dissertation investigates post-settlement events (i.e. intra- and inter-specific interactions, behaviours, and microhabitat use) that affect spatial dynamics (i.e. space use and movement) in Caribbean labrids. Six chapters on various aspects of labrid spatial dynamics and assemblage structure are presented. Extensive background information is provided for each chapter separately, so the purpose of this general introduction is to provide an outline for the dissertation.

Caribbean Labrids

There are fifteen labrid species in the Caribbean region (Bohlke and Chaplin 1968). Although specimens of thirteen of these fifteen species were observed in St. Croix, only six species were amenable to visual censusing and the purposes of this research. The nine species that were excluded are either turtle grass inhabitants (i.e. razorfishes (*Xyrichtys*)), or larger, solitary individuals that have large home ranges (i.e. hogfishes (*Bodianus* and *Lachnolaimus*)), or they are

very rare in St. Croix (i.e. the dwarf wrasse (*Doratonotus megalepis*)). Of the six species that were included, five swim in loose, mixed aggregations with heterospecifics (the slippery dick wrasse (*Halichoeres bivittatus* (Bloch)), the yellowhead wrasse (*H. garnoti* (Valenciennes)), the clown wrasse (*H. maculipinna* (Muller and Troschel)), the black ear wrasse (*H. poeyi* (Steindachner)), and the puddingwife wrasse (*H. radiatus* (Linnaeus))). The sixth species, the bluehead wrasse (*Thalassoma bifasciatum* (Bloch)), predominantly swims in large schools of conspecifics slightly above the reef, but occasionally uses the reef for shelter and also swims in loose aggregations with heterospecific labrids.

CHAPTER II: Home range size and activity centers

The first chapter investigates home range area requirements for labrids and their life stages (juveniles, initial phase adults, and terminal phase adults). There has been a general trend reported for high site fidelity and long-term site attachment in many coral reef fish species (Bardach 1958, Springer and McErlean 1962, Sale 1971, Ogden and Buckman, 1973, Ehrlich 1975, Fitch and Shapiro 1990, Wootton 1990, Holland, Peterson, Lowe & Wetherbee 1993). The goals of this chapter are: 1) to confirm the sedentary nature of several labrid species, 2) to acquire a better understanding of how these species utilize space on the reef, and 3) to examine the relationship between home range area and fish size in these species. An additional objective of this study is to investigate how these fish proportion their time within their home ranges. Do they allocate their time randomly within their home ranges, or are activities concentrated into core use areas?

CHAPTER III: Intra- and inter-specific overlap in behaviour

The second chapter investigates labrid behaviour and social interactions. Before investigating the effects of behaviour and social interactions on the spatial arrangements of labrid home ranges, it is necessary to initially identify important behaviours in their daily time budgets. A second focus of this chapter is whether species and life stages could be correctly predicted based on

the behaviours recorded. The questions addressed include: 1) Are there behaviours that separate labrid species? 2) Are there behaviours that separate life stages within a species? and 3) Do these species go through similar ontogenetic shifts in behaviour as they mature?

CHAPTER IV: Distribution of behaviours throughout home ranges

The main purpose of this chapter is to integrate an examination of space use with observations on behaviour and social interactions. This can be separated into specific questions: 1) Do these labrids feed or swim alone more frequently in the core use areas of their home ranges compared to peripheral regions? 2) Do the core use areas provide refuges from agonistic encounters with damselfish? 3) Are labrids assembled with other fishes more often in the center or in the peripheral part of their home range?

CHAPTER V: Intra- and inter-specific overlap in microhabitat use

These labrids have been the focus of many ecological studies (e.g. Roede 1972, Warner et al. 1975, Warner and Robertson 1978, Thresher 1979, Robertson 1981, Wainwright 1988). However, microhabitat overlap among juvenile, initial phase, and terminal phase conspecifics, and among heterospecifics has never been closely investigated. These sympatric labrids are demersal, site-attached fishes in which conspecific life stages and heterospecifics extensively overlap and interact within reef habitats. This chapter addresses three specific questions: 1) Within these habitats, are microhabitats partitioned among the different species? 2) Do juveniles prefer more sheltered microhabitats than adults? and 3) Do these labrids show random microhabitat use, or are they selective?

CHAPTER VI: Interactions with territorial pomacentrids

The main objective of this chapter is to determine the effects of the presence of territorial pomacentrids, *Stegastes leucostictus*, on the home range parameters, spatial dynamics, and behavioural interactions of *Halichoeres bivittatus*. Pomacentrids are known to be very aggressive

towards conspecifics or heterospecifics entering their territories (Sale 1971; Clarke 1977; Itzkowitz 1977a,b; Thresher 1984; Ebersole 1985; Allen 1991; Santiago and Castro 1997). The strongest attacks are directed at potential egg predators, including many labrid species, which have the greatest relative impact on the reproductive success of the damselfish (Reinboth 1973; Katzir 1981; Ferreira et al. 1998). In many pomacentrids, it has been demonstrated that individuals are capable of discriminating between species; subsequently, their level of aggression towards different species that invade their territories can be modified accordingly (Myrberg and Thresher 1974; Katzir 1981; Ferreira et al. 1998). *Stegastes leucostictus* can apparently distinguish among approximately 50 different species of reef fishes that intrude on its territory (Ebersole 1977). Consequently, this chapter addresses whether or not *H. bivittatus* show fluid, or plastic changes in their home range boundaries after *S. leucostictus* are introduced into the center of adult home ranges, or adjacent to juvenile home ranges. It is hypothesized that damselfish introductions compared to control treatments would cause the focal individual *H. bivittatus* to do any or all of: 1) reduce their home range area, 2) relocate their home range position, 3) use alternative microhabitats, 4) increase the amount of time spent interacting with damselfish, which would subsequently decrease the amount of time spent foraging or in foraging assemblages, and 5) swim higher above the substrate in order to avoid encounters with the introduced damselfish.

CHAPTER VII: Environmental factors that affect labrid assemblage structure

This chapter investigates whether small scale processes (i.e. on the scale of the individual home range) investigated in previous chapters lead to predictable patterns in the distribution of labrid populations at larger scales. In other words, do relationships between individual labrids and their microhabitat requirements result in detectable correlations between labrid abundances and microhabitat availability on a larger spatial scale? Additionally, a related purpose of this chapter is to determine environmental factors that affect labrid assemblage structure. Reef characteristics

that are included as environmental factors in the analyses consisted of: 1) reef zone, 2) depth within a zone, 3) microhabitat availability, 4) topographic complexity, and 5) population abundances of territorial damselfish species. Through visual censuses and quantification of environmental parameters, general differences in labrid assemblage structure and environmental effects are determined. Canonical Correspondence Analysis is then used to determine the degree of associations between patterns of abundance of labrid species and their life stages, and environmental parameters.

CHAPTER II

HOME RANGE SIZE AND ACTIVITY CENTERS IN SIX SPECIES OF CARIBBEAN WRASSES (FAMILY LABRIDAE)

ABSTRACT

Similar to many terrestrial animals, tropical and temperate reef fishes often exhibit high site fidelity and long-term site attachment. In many of these species, there is a positive relationship of fish size to home range area. This study examines the relationship between fish size and home range area in six Caribbean wrasse species (Family Labridae) including: *Halichoeres bivittatus*, *H. garnoti*, *H. maculipinna*, *H. poeyi*, *H. radiatus*, and *Thalassoma bifasciatum*. Regression analyses revealed similar relationships between home range area and fish size for four of the six wrasse species. *Halichoeres bivittatus*, *H. garnoti*, *H. radiatus*, and *Thalassoma bifasciatum* all appeared to have the same rate of increase in home range area with increasing fish size. Upon closer investigation of this relationship for three of these species (excluding *H. radiatus* because only juveniles were investigated), I found that once individuals reach the initial phase, home range area reaches a plateau. Although juveniles have smaller home ranges and core activity areas than initial phase (IP) adults and terminal phase individuals, it is not simply because of their smaller lengths. After accounting for differences in fish length, IP adults require larger areas than juveniles per cm of fish length, and terminal phase adults require larger areas than IP adults. In other studies where evidence for this relationship between size of animal and home range area has been found, it has also been commonly observed that activities are concentrated into core use areas

containing important resources such as food, nests, and shelters. This study also examined the relative size of activity centers compared to total home range area. It was found that 50% of the observation points were found in 13-26% of the home range area. There was a high consistency in this relationship for all species and life stages studied. *Halichoeres bivittatus* juveniles exhibited the smallest ratio of activity center area to total home range area, and was the only species for which this ratio was significantly different between life stages.

INTRODUCTION

The patterns of spatial dynamics in individuals (i.e. space use and movement) can be considered one of the most important demographic parameters influencing the structure of populations and communities (Luckhurst and Luckhurst 1978, Samoilys 1997, Barrett 1995, Zeller 1997). Studies on the occupancy of specific shelter sites or home range areas can assess their importance as a stabilizing influence on population and community structure (Sale 1971, Smith and Tyler 1972, Luckhurst and Luckhurst 1978). This study investigates the space use and home range area requirements of several coral reef fish species in the Labridae: *Halichoeres bivittatus*, *H. garnoti*, *H. maculipinna*, *H. poeyi*, *H. radiatus*, and *Thalassoma bifasciatum*. The term “home range” in this study was defined as the area in which an animal spends its typical activity cycle, whereas the term “territory” implies active defense of the total or partial home range area. Knowledge of home range and territory use in coral reef fish species is important to the use and effectiveness of marine reserves in managing fish populations (Samoilys 1997, Kramer and Chapman 1999).

There has been a general trend reported for high site fidelity and long-term site attachment in many coral reef fish species (Bardach 1958, Springer and McErlean 1962, Sale 1971, Ogden and Buckman, 1973, Ehrlich 1975, Fitch and Shapiro 1990, Wootton 1990, Holland, Peterson,

Lowe and Wetherbee 1993). Representative fishes from many reef fish families have been the focus of numerous home range investigations (a list of these species and estimates of home range areas have been compiled in Table 2.1). Possession of home ranges or territories offers the advantage of familiarity with a section of the reef and consequent knowledge of the location of feeding, sleeping, shelter sites, and potential competitors (Wootton 1990, Barrett 1995, Kramer and Chapman 1999). Earlier studies on space use in reef fish focused on small, demersal, and typically territorial fishes from several families, including: Pomacentridae (Low 1971, Sale 1971, Keenleyside 1972), Gobiidae (Luckhurst and Luckhurst 1978), and Blenniidae (Nursall 1977) (See Table 2.1). Recently, space use studies have broadened to include fishes from numerous other families that are less substrate-oriented, including: Serranidae, (Shapiro, Garcia-Moliner and Sadovy 1994, Samoilys 1997, Zeller 1997), Scaridae (van Rooij et al. 1996), and Labridae (Barrett 1995, Nemtsov 1997). Although several labrids in this study have been studied extensively (e.g. Roede 1972, Reinboth 1973, Thresher 1979, Warner and Robertson 1978, Robertson 1981) not much is known about the space use and home range requirements of these Caribbean species.

Space use and home range size can be influenced by a variety of factors including diet and foraging (Smith and Tyler 1972, Dill et al. Fraser 1981, Davies and Houston 1984, Norman and Jones 1984, Wauters and Dhondt 1992, Hews 1993, Coleman and Wilson 1996), predators (Clarke et al. 1993), habitat (Smith and Tyler 1972, Eason and Stamps 1992), intraspecific interactions (Brown 1969, Schoener and Schoener 1982, Davies and Houston 1984, Norman and Jones 1984), interspecific interactions (Wauters and Gurnell 1999, Jones *in review*), and other social factors (Eifler 1996, Melville and Swain 1999). Many studies have indicated that home range size seems to be largely a function of resource requirements (McNab 1963, Christian and Waldschmidt 1984, Gerking 1994). Terrestrial vertebrates commonly respond to increases in food

availability by decreasing home range size (Boutin 1970). This relationship is a part of the Optimal Foraging Theory argument that food density and territory size are inversely related. Alternatively, food may not be the primary variable influencing home range size (Ebersole 1980, Robertson 1981, Gerking 1994, Melville and Swain 1999). Indeed, some studies have found that resources can be completely unrelated to territory sizes (Southern and Lowe 1968, Seastedt and MacLean 1979). According to Robertson (1981), studies on territory use in coral reef fishes have not found any simple relationship between territory size and resource density.

Another common relationship in the spatial arrangement of animals is that home range size tends to increase with body size (Schoener 1968, Simon 1975, Larson 1980). This relationship exists within a species (Cole 1984, Barrett 1995, Matsumoto et al. 1999, Overholtzer and Motta 1999) as well as across species within a taxon (Sale 1978, Kramer and Chapman 1999) simply because larger animals typically require greater amounts of space and resources. This relationship has been observed in fish species from many different families, including Gobiidae (Cole 1984), Labridae and Monacanthidae (Barrett 1995), and Scaridae (Overholtzer and Motta 1999) as examples. Although this positive relationship between body size and home range area is very common in fishes, it is not a universal rule. For example, Samoilys (1997) found a seasonal relationship between fish size and home range area in the coral reef fish, *Plectropomus leopardus* (Serranidae). In the spring, there was a linear relationship between fish size and area of movement; however, in the other seasons, there was no correlation. Another investigation with the same species did not find any correlation, seasonal or otherwise, between home range area and fish size (Zeller 1997). A study on two temperate labrids found that home range size was positively correlated with total length in one species, *Pseudolabrus eoethinus*, but not in the other species, *P. sieboldi* (Matsumoto et al. 1999). Additionally, there were no correlations between fish size and home range or territory size for the following fishes: the territorial rocky reef fish, *Parma victoriae*

(Family Pomacentridae) (Norman and Jones 1984); the freshwater fish, *Barbus haasi* (Aparicio and de Sostoa 1999); and the temperate rocky reef fish, *Cheilodactylus fuscus* (Family Cheilodactylidae) (Lowry and Suthers 1998).

This study investigates the relationship between fish size and home range area in six labrid species. The software program CALHOME (Kie et al. 1994) was used to calculate estimates of home range size using two methods: the minimum convex polygon method (Mohr 1947), and the adaptive kernel method (Worton 1989). This study also takes a closer look at the distribution of activity points within a home range by examining the area coverage of centers of activity. Most studies of fish home ranges have focused on size and overlap of home ranges rather than on activity patterns within these ranges.

Activity within home ranges is often concentrated into core areas containing important resources such as nests, refuges, or food sources (Warden and Lorio 1975, Chilton and Poarch 1997, Zeller 1997). For example, Warden and Lorio (1975) found that individual largemouth bass had several localized home range areas within larger movement areas where they spent most of their time. A telemetry study by Zeller (1997), illustrated a preference for a small number of locations within a larger home range area in the coral trout, *Plectropomus leopardus* (Serranidae). Similar investigations with lizards have yielded similar results. For example, Melville and Swain (1999) found that all of their study lizards possessed multiple activity centers within their home ranges, and Eifler (1996) calculated that the lizard species he studied had areas of concentrated activity that averaged about one-tenth of the total home range size.

The goals of this study were: 1) to confirm the sedentary nature of several reef fishes of the Family Labridae, 2) to acquire a better understanding of how these species utilize space on the reef, and 3) to examine the relationship between home range area and fish size in these species. An additional objective of this study was to investigate how these fish proportion their time within their

home ranges. Do they allocate their time randomly within their home ranges, or are activities concentrated into core use areas? Data were obtained through direct visual observations of different individuals from each labrid species.

METHODS

Study Site

All home range maps were recorded while snorkeling on contiguous stretches of the back reef area of Tague Bay, St. Croix, U.S.V.I. (17° 36'N, 64° 36'W). The back reef ranged in depth from 3-6m at its base to a partially exposed reef crest at low tide. Most fish observations were carried out at a depth of 2 m. Algae growing on coral rubble (algal turf) was the predominant substratum, followed by dead *Porites porites*, dead *Acropora palmata*, other broken pieces of dead coral, and sand. Other live corals such as *Siderastrea* spp., *Diploria* spp., and *Agaricia* spp., as well as gorgonians, sponges, and seagrass beds occurred but were less common. These studies were carried out from May-August in 1998 and 1999.

Study Organisms

Juveniles and adults of the following labrid species were studied: *Halichoeres bivittatus*, *H. garnoti*, *H. maculipinna*, *H. poeyi*, and *Thalassoma bifasciatum*. Only juveniles were observed for *H. radiatus* because the adults are much larger than the other species, and are less sedentary. Adult *H. radiatus* commonly roam large reef areas with parrotfishes (Scaridae) and goatfishes (Mullidae), and retreat quickly from divers.

These closely related labrid species are morphologically very similar, but easily identified by colour differences (Bohlke and Chaplin 1968, Roede 1972, Warner and Robertson 1978, Humann 1996). In many labrid species, there is a strong relation between colour pattern and body length (Roede 1972). Colour patterns may sometimes be used to separate individuals within a

species into the various life history stages. With the exception of *H. radiatus*, the three life history stages characterized for all of the species in this study were juveniles, initial phase (IP), and terminal phase (TP). All labrid species in this study are protogynous hermaphrodites (Warner and Robertson 1978). Initial phase males are usually primary (those born as such), but rarely secondary (females that have changed sex to become males). Terminal phase individuals are typically larger primary or secondary males that change colour, social status, and some behaviours to become TP individuals (e.g. terminal phase *T. bifasciatum* individuals are involved in pair spawning, whereas IP individuals are involved in group spawns (Fedderm 1965)). It is generally the larger fish in a local population that become TP individuals, and they are often vastly outnumbered by IP individuals. Socially, TP individuals become territorial during spawning, and they are often pair spawn with numerous females that reside within the large TP home ranges.

Halichoeres radiatus, *H. garnoti*, and *H. maculipinna* juveniles have different colour patterns from IP individuals and discrimination of life stages was based on colour. In the other species where there were no changes in colour patterns between juveniles and IP individuals, juveniles were defined as those individuals between 20mm and 40mm in total length (*c.f.* Warner and Robertson (1978)). Initial phase individuals were distinguished from TP individuals through colour differences and morphological differences.

Additional information about the social and mating systems of the *Halichoeres* species has been described in the following studies: Warner and Robertson (1978), Thresher (1979), Robertson (1981), and Petersen (1991). The ecology and social system of *Thalassoma bifasciatum* have been studied extensively (Fedderm 1965, Warner and Hoffman 1980, Fitch and Shapiro 1990). Fitch and Shapiro (1990) provide a good description of the different phases of hermaphroditism. Some studies on the behaviour of *T. bifasciatum* demonstrated that it is a migratory spawner with no permanent home ranges except for actively defended spawning territories of TP males (Warner and

Hoffman 1980). However, Fitch and Shapiro (1990) found a variant social structure where individuals occupy permanent home ranges that are not actively defended, and they spawn within or near these home ranges. Many *T. bifasciatum* on the contiguous back reef areas of Tague Bay, St. Croix, were found to possess permanent home ranges that were not actively defended (*pers. obs.*). It is possible that *T. bifasciatum* at this location may have two phases of movement; however, only those that possessed home ranges were included in this study.

Initially in 1998, individual fishes of all species were caught with a lift net (see Roede 1972) and tagged with beaded Floy® anchor tags to verify their sedentary nature. Tagging fishes of measured size and releasing them also allowed us to test the accuracy of my visual estimates of total fish length. Estimates of fish length (to within 0.5 cm) were practiced until my estimates did not differ from actual lengths (Kolmogorov-Smirnov: $p = 0.36$; $n = 35$; following the methods of Bell et al. 1985). The fishes were anaesthetized with clove oil prior to tagging (Munday and Wilson 1997). The fishes quickly regained consciousness and resumed normal behaviours. In fact, one IP adult *T. bifasciatum* joined a group spawn less than 5 minutes after recovery (*pers. obs.*). Therefore, tagging did not appear to greatly influence the behaviour of labrids. After these preliminary investigations, however, I found that individual labrids could be reliably identified without catching and tagging by recognizing differences in facial markings, lateral line deformities, and/or size differences.

Home Range Mapping

In order to observe space use in juvenile and IP individuals, quadrats (10x10 m²) were randomly marked on the reef with flagging tape. The habitat features of each quadrat were mapped on a slate. Mylar film was then placed over the map to record the positions of an individual fish during each observation period. Observation periods occurred between 0800 hr and 1600 hr, which appeared to be the peak activity periods for labrids on the reef. Observation

periods were aborted if the focal individual was involved in extensive spawning behaviours (which often occurs outside of the normal home range area). Observations were also not carried out on days when visibility fell below 30ft (during storm events or algal blooms), because the fish appeared to behave abnormally. Individual fishes were randomly selected from each quadrat for observation. Each observation period lasted for 10 minutes, and at every 20 second interval, the position and several aspects of the behaviour of the focal fish were recorded (for a total of 30 points per observation period). Only the home range measurements will be discussed in this study. Behaviours, species interactions, microhabitat use, and swimming distance above the substrate are presented in another study (Jones, *in preparation*). To improve my estimates of home range area, I used repeated observations on focal individuals. A minimum of four observation periods were recorded for each focal individual in this study, resulting in a minimum of 120 observation points per focal individual (spread out over a period of approximately two weeks per individual). In a preliminary study, I found that an additional set of observations did not affect the size of the home range area estimated from four sets (Mann Whitney T = 986.00; $p = 0.812$). Thus only four sets of observations were conducted on subsequent focal individuals.

Because TP adults have larger home ranges than IP adults and juveniles, it was very difficult to construct habitat maps on which to track their movements. Instead, TP individuals were identified by distinctive markings and size, and followed repeatedly during 4 separate 10-minute observation periods. During these observation periods, I followed the TP individual while unwinding a tape measure behind me. At the end of the 10-minute period, I recorded the total length of tape measure used, and I also measured the maximum length and width of the home range area. In this study, the length and width dimensions were multiplied together to get a rough estimate of home range area for TP individuals.

Home Range Calculations

The recorded positions of juveniles and IP individuals were transferred into Cartesian coordinates and then analysed in the program CALHOME (Kie et al. 1994). CALHOME was used to calculate the home range area and core use areas through the adaptive kernel (AK) (Worton 1989) and minimum convex polygon (MCP) methods (Mohr 1947). Examples of results from the two methods of calculating the point percentage contours (50%, 75%, and 95%) for home range areas are given in Fig. 2.1 and Fig. 2.2. For adaptive kernel estimates, the bandwidth and smoothing parameters were not preset; instead, by default, the program estimates an optimal bandwidth. The smoothing parameter (which creates point percentage contours, or bandwidths) for the AK method is affected by the distribution or clustering of the observation points. It changes with the density of points, so areas with a high concentration of observations are smoothed more. The resultant point percentage contours delineate areas of probable visitation that may extend beyond the areas of actual visitation (Worton 1989).

Because animals occasionally make exploratory excursions outside their areas of normal activity, the home range is commonly specified as an area within which some fixed percent of activity falls (most often 95%)(Anderson 1982; Worton 1989). This study employs calculations of the 50%, 75% and 95% point percentage contours (see Fig. 2.1 and Fig. 2.2 for examples). The 50% contour delineates the core use area (as per Eifler 1996). Minimum Convex Polygon calculations are not intended as a method of identifying centers of activity or core areas of animal home ranges (Gallerani Lawson and Rodgers 1997), and a substantial difference in the core use areas delineated by the Minimum Convex Polygon method and the Adaptive Kernel method is seen in Fig. 2.2. Hence, core use analysis in this paper is conducted only with the AK method. In cases where more than one activity center was delineated, the area of each activity center was combined to give the total core use area.

Statistical Analysis

To determine the relationship between home range area and fish size, regression analyses were performed on \log_{10} (home range area) versus \log_{10} (fish size). All analyses were carried out with SYSTAT version 8.0. The 95% contour estimates from the minimum convex polygon and adaptive kernel methods were used as home range areas for the regression analyses. Only juvenile and IP data were used in these analyses because the method of estimating home range area for TP individuals was different. Prior to analysis, home range area and fish size (total length in cm) were \log_{10} transformed to improve normality and homogeneity of variances. To determine if the relationship between fish size and home range area varied among species, an ANCOVA was run with species as the main factor, and \log_{10} (fish size) as the covariate (following the procedures given in Huitema (1980)). A significant interaction between species and \log_{10} (fish size) would indicate that this relationship varies with species.

The ANCOVA detected differences in the relationship between fish size and home range area ($p = 0.046$); however, *Halichoeres bivittatus*, *H. garnoti*, and *H. radiatus*, and *Thalassoma bifasciatum* were not significantly different from one another (intercept and slope tests; SYSTAT GLM procedure; $p > 0.05$). These three species (excluding *H. radiatus* because only juveniles were investigated) were pooled to determine if the relationship between fish size and home range area is as strong within life stages as it is when all life stages are considered together. Regression analyses with the three species pooled were performed for juveniles + initial phase adults, juveniles alone, and initial phase adults alone. This investigated whether or not home range area reaches a plateau once individuals become initial phase adults, despite their continued growth.

To take a closer look at the effects of life stage, species, and fish length on activity centers and home ranges, separate 2-way ANOVAs were used to look at differences in activity center area (= AK 50%), total home range area (= AK 95%), m^2 area requirements per cm of fish length (=

AK 95% / fish total length), and the ratio of activity center area to 95% home range area (AK 50% / AK 95%). The main effects in each model were life stage (juveniles or initial phase adults), and species (all species except *H. radiatus*). Significant interactions between life stage and species indicated that the yield variable behaves differently for different species between the life stages. Qualitative comparisons can be made for the values of AK 95% estimates and {AK 95% / fish total length} among all three life stages (TP individuals were not included in the statistical analyses because home range area estimates were made with a different method, and the sample sizes were very small).

Adaptive Kernel 50% and AK 95% estimates of home range area were \log_{10} transformed prior to analysis to normalize the data and homogenize the variances. The average area required per cm of fish (AK 95% / fish total length) was also \log_{10} transformed prior to analysis to meet the same criteria. Analysis of this response variable investigated the effect of life stage on home range area after accounting for differences in fish length. The final analysis investigated the area coverage of activity centers. Dividing the 95% AK home range area by the 50% AK core use area, gives the ratio of area covered by 50% of the observation points. The smaller the ratio, the more concentrated or tightly clustered the points are within the core use area. These data were angular transformed prior to analyses to meet the assumptions of normality and homogeneity of variances. Significant effects of the main factors were followed by Tukey's multiple comparison tests to determine where specific differences could be detected among species within life stages.

RESULTS

Home range size versus fish size

One obvious and unsurprising result was that initial phase adults possess larger home ranges than juveniles, as shown by the positive log-log relationship between fish size and 95% home range area (MCP, Fig. 2.3; AK, Table 2.2). As juveniles grow, their requirements for home range area increases. This relationship is significant for all species at $p < 0.001$ except *H. radiatus*, for which $p = 0.014$ (for MCP data; $p = 0.007$ for AK data). The \log_{10} - \log_{10} regression analyses also revealed that the proportion of variance in home range size explained by fish size differed among the species (r^2 values varied from 0.44-0.91 (MCP data); and 0.40-0.90 (AK data)). The MCP method yielded different estimates than the AK method, and the differences between the methods were inconsistent among the species. Fish size accounted for 90-91% of the variation in home range size for *Halichoeres bivittatus*, 57-64% for *H. garnoti*, 40-44% for *H. maculipinna*, 40-55% for *H. poeyi*, 45-53% for juvenile *H. radiatus*, and 61-65% for *Thalassoma bifasciatum*.

Although all species showed significant relationships between \log_{10} (fish size) and \log_{10} (home range size), this relationship varied among the species. The ANCOVA with \log_{10} (home range area) as the response variable revealed a significant interaction between the main factor, species, and the covariate, \log_{10} (fish size) ($p = 0.046$). To determine which species differed in their relationship between fish size and home range size, multiple comparisons were performed through the GLM procedure for contrasts of slopes and intercepts in SYSTAT 8.0. *Halichoeres maculipinna* had a significantly larger intercept than *H. bivittatus* ($p < 0.001$), *H. garnoti* ($p = 0.006$), and *H. radiatus* ($p = 0.047$). *Halichoeres maculipinna* and *H. poeyi* both had significantly lower slopes than *H. bivittatus* ($p = 0.005$ and $p = 0.049$, respectively). This relationship was not significantly different among *Halichoeres bivittatus*, *H. garnoti*, *H. radiatus*,

and *Thalassoma bifasciatum*.

To discern if the relationship between fish size and home range area is as strong within a life stage as it is when life stages are combined, the species that were not significantly different in the ANCOVA (*Halichoeres bivittatus*, *H. garnoti*, and *Thalassoma bifasciatum*) were pooled for additional regression analyses (Fig. 2.4, Table 2.3). (*H. radiatus* was excluded because only juveniles were investigated). This tested whether home range area continues to increase as juveniles become initial phase adults. When the three species were pooled, there was a highly significant relationship between \log_{10} (fish size) and \log_{10} (home range size) for the combined data from juveniles and initial phase adults (MCP: $p < 0.001$, Fig. 2. 4; AK: $p < 0.001$, Table 2.3). For these two life stages combined, fish size explained 75% of the variation in home range area (74% for AK). For juveniles alone, there was still a significant relationship ($p < 0.001$ for MCP and AK) although fish size explained a low amount of the variation in home range area (MCP: $r^2 = 0.23$, Fig. 2.4; AK: $r^2 = 0.19$, Table 2.3). However, the regression of \log_{10} (fish size) on \log_{10} (home range size) for initial phase adults was non-significant (MCP: $p = 0.31$, Fig. 2. 4; AK: $p = 0.21$, Table 2.3), and fish size only explained 0.09% of the variation in home range size (0.9% for AK). It appears as though once juveniles reach the initial phase, their home range areas reach a plateau, despite continued growth.

Differences in Activity Center Area and Home Range Size Among Species and Life Stages

Initial phase adults possess larger activity centers (50% AK point percentage contour) than juveniles (Fig. 2.5). Within a species, the activity centers of initial phase adults were always significantly larger than juveniles (ANOVA, $p < 0.05$). There was a significant interaction between species x life stage ($p < 0.001$). For juveniles, *H. maculipinna* had significantly larger core use areas than all species analysed except *H. garnoti*; and *H. bivittatus* juveniles had significantly smaller core use areas than all species analysed ($p < 0.05$: Tukey's *post hoc* tests).

There were no significant differences in core use area among the species for IP adults ($p > 0.05$). On average, core use areas ranged from 0.6 - 5.3m² for juvenile labrids; whereas IP adult core use areas ranged from 5.4 - 8.2m².

Initial phase adults had significantly larger home range areas (95% AK) than juveniles (ANOVA, $p < 0.05$; Fig. 2.6). Terminal phase adults had qualitatively larger home range areas than IP adults. Total home range areas (95% AK) ranged from 4.2 to 22.6m² for juveniles, 26.5 to 48.8m² for IP adults, and approximately 102 to 162m² for terminal phase adults (recall that TP estimates were obtained through different methods and were comprised of smaller sample sizes, hence their exclusion from statistical analyses). There was a significant interaction between species x life stage ($p = 0.011$). For differences among species within the life stages, the results were the same as the multiple comparison tests for core use area.

Home range area requirements after accounting for differences in fish length

Although juveniles have smaller home range areas than adults, it is not simply because of their smaller length. By calculating the ratio of home range area / fish size, this reveals the amount of home range area required per centimeter of fish (Fig. 2.7). Centimeter for centimeter of fish, IP adults require significantly larger home range areas than juveniles ($p < 0.05$, ANOVA), and TP adults require qualitatively much larger home range areas than IP adults. There was no significant interaction between species x life stage ($p = 0.085$), suggesting that the differences among species are consistent across life stages. *H. maculipinna* and *T. bifasciatum* are both significantly different from the other three species analysed, but not significantly different from one another (results of Tukey's *post hoc* tests of multiple comparison). Requirements of home range area per cm of fish ranged from 1.2 - 3.4 m² per cm of fish for juveniles, 2.6 - 4.8 m² per cm of fish for IP adults, and 7.8 - 11.3 m² for TP adults.

Concentration of observation points in activity centers

To determine if activities are randomly distributed throughout labrid home ranges, the ratio of AK50% (the activity center) to AK 95% (which represents the total home range area) was calculated. Smaller values for this ratio indicate that the observation points in the activity center are closer together; in other words, the 50% point percentage contour encompasses a smaller percentage of the home range area. This ratio ranges from 0.13 for *Halichoeres bivittatus* juveniles to 0.26 for *H. radiatus* juveniles. This can be interpreted to mean that 50% of the observation points are found in 13-26% of the home range area. Therefore, in the other 74-87% of the home range area, there is a large spread of the other 50% of the observation points. This ratio is fairly consistent for all labrids and life stages in this study. However, the activity centers of *H. bivittatus* juveniles cover significantly smaller proportions of their home ranges than the other species except *Thalassoma bifasciatum*. There was a significant interaction between species x life stage ($p = 0.023$, ANOVA), which is attributed to the highly significant difference between juvenile and IP adult *H. bivittatus* ($p < 0.001$). There was no significant difference among species within the IP adult stage ($p > 0.05$).

DISCUSSION

Observations of space use by Caribbean labrid species provided evidence of their sedentary nature and high site fidelity. This study also revealed strong relationships between fish size and home range area. This relationship varied among species, from a low of 44.3% of the variation in home range area explained by size of *Halichoeres maculipinna*, to a high of 90.9% for *H. bivittatus* (MCP data; Fig. 2.3). Upon closer investigation, it was found that home range area requirements appear to plateau after juveniles enter the initial phase (for *Halichoeres bivittatus*, *H. garnoti* and *Thalassoma bifasciatum*). There also appears to be a large difference in requirements

for space between initial phase and terminal phase adults. Beyond the initial phase, there may be more important factors other than fish size influencing home range area (e.g. social factors).

This study also revealed some interesting results about the distribution of observation points within the home range areas. There is evidence to suggest that these labrids do not distribute their activities randomly throughout their home ranges. Instead, they appear to concentrate their activities into core use areas. The establishment of activity centers, and the percent area coverage of the home range by these centers appears to be a highly consistent pattern for all species studied.

Approach used to study home range parameters

The approach taken in this study to estimate home range area combines suggestions from previous studies on improving precision and accuracy (Rooney et al. 1998, de Solla et al. 1999). The methods employed to estimate home range in this study involved sampling the focal individual's position at fixed time intervals for a set period of time (every 20 seconds for 10 minutes), and then performing repeated observations over a longer time scale (up to a 2 week sampling period). Rooney et al. (1998) conducted a study to look at autocorrelation in home range studies and found that the correct strategy for the best possible estimation of home range size is the repeated use of as short a sampling interval as possible over an extended period of time. de Solla et al. (1999) analysed the effect of autocorrelation on home range estimates, and suggested that autocorrelation is not damaging to home range measurements; however, their recommendations are similar to those of Rooney et al. (1998), by suggesting a decrease in the time intervals between successive observations. Nevertheless, the estimates of home range area in this study appeared to be accurate and reliable enough to compare space use across these labrid species, and to look at the distribution of observation points within the home range area.

This study also employed Adaptive Kernel and Minimum Convex Polygon methods of

calculating home range area and found differences between them. Both of these methods use point percentage contours which means the software program performing the calculations considers the distribution of points in space and delineates contours (the percentage is set by the user) around the points based on nearest neighbour distances (for MCP), or the density/clustering of points (for AK). There are advantages and disadvantages to both of these methods. For example, minimum convex polygon has a sample size bias (Jennrich and Turner 1969), and it assumes that home range shape is convex. Another drawback is that the MCP method tends to cut out much of the areas of actual visitation due to the strictly linear polygonal boundaries. With a small sample size, however, MCP is easy to calculate. The Adaptive Kernel method, on the other hand, uses smoothing parameters to calculate the probability distribution that describes where the animal might be during a single, randomly chosen time within the period of interest (Worton 1989). The smoothing parameters are affected by the distribution or clustering of the observation points. They change with the density of points, so areas with a high concentration of observations are smoothed more. The resultant percentage contours delineate areas of probable visitation that may extend beyond the areas of actual visitation (Worton 1989). The drawback to using the AK method is that it requires a large sample size (not very effective for mark-recapture studies). There were inconsistent differences in home range area estimates between the methods, which emphasizes the necessity of reporting the methods used.

Relationship of fish size to home range area

Strong correlations between fish size and home range area have been found in other fishes (e.g. Cole 1984, Barrett 1995, Overholtzer and Motta 1999). Cole (1984) found that territory size was directly correlated with fish size in the temperate marine goby, *Coryphopterus nicholsi* (Family Gobiidae). Barrett (1995) found this relationship in four of the six temperate reef species he studied (Families Labridae and Monacanthidae). Overholtzer and Motta (1999) found that

home range size was a function of fish size for two of the three juvenile scarids they observed. They found that fish size explained 60 - 68% of the variation in home range size.

Although the ecology and social systems of many of the labrid species used in this study have been intensively examined, we had limited knowledge about their home range requirements prior to this study (with the exception of *Thalassoma bifasciatum*, Fitch and Shapiro (1990)). I found a strong relationship between fish size and home range area, with a plateau in three of the six species once juveniles reach the initial adult phase. There was also a large difference in home range requirements between IP and TP individuals, even after fish length was taken into account. Other factors that can affect home range size include habitat geometry and the composition of neighbours or other social factors (Stamps et al. 1987). The large difference in home range area between IP and TP individuals in this study may be due to the harem social structure with the home range of one terminal phase male encompassing many home ranges of subordinate individuals. More research is needed concerning the spatial dynamics of terminal phase individuals.

In terms of space use and specific microhabitat requirements, it is known that labrids generally require some minimal area of sand within their home range (Bohlke and Chaplin 1968, Nemtzov 1997). Beyond that, there are no particular microhabitat associations noted in the literature except that *Halichoeres poeyi* tends to be associated with seagrass and macroalgae because of its green colour (Bohlke and Chaplin 1968). Labrids generally bury themselves in the sand at night to sleep, or to quickly evade predation. In another Caribbean labrid, the green razorfish, *Xyrichtys splendens*, it has been observed that each individual maintains a small "dive site" in coarse, sandy substrates, into which the fish repeatedly dives to keep it soft and to facilitate future predator avoidance (Nemtzov 1997). Beyond the use of sand patches and seagrass beds by *H. poeyi*, however, microhabitat availability and use within labrid home ranges has been

investigated by Jones (in preparation). I have found that microhabitat configuration does not appear to be the primary factor influencing home range position, shape, or size.

Differences among *Halichoeres maculipinna* and the other labrids studied

The regression analyses revealed differences in the relationship between fish size and home range area among the species studies. *Halichoeres maculipinna* had a significantly larger intercept than *H. bivittatus*, *H. garnoti*, and *H. radiatus* which suggests larger home range areas for *H. maculipinna* compared to heterospecifics of the same length. *Halichoeres maculipinna* and *H. poeyi* both had significantly lower slopes than *H. bivittatus*, which suggests that as *H. maculipinna* and *H. poeyi* grow, their requirements for home range area do not increase as rapidly as that of *H. bivittatus*. The results of 2-way ANOVAs on AK estimates of home range area revealed some different results from the regression analyses. The 2-way ANOVAs before accounting for differences in fish length revealed no differences in home range area among IP adults, whereas *H. maculipinna* juveniles had significantly larger home range areas than all species analysed except *H. garnoti*. After accounting for differences in fish length, both *H. maculipinna* and *Thalassoma bifasciatum* have larger area requirements per centimeter of fish length than the other species analysed. Consequently, the only consistent difference among the different analyses was that *H. maculipinna* appear to have a different relationship between fish length and home range area than the other labrids studied. Increased observations may help clarify some of the differences among species and life stages with respect to home range requirements.

One possible explanation for the difference between *H. maculipinna* and the other species is due to behavioural differences. Qualitatively, *Halichoeres maculipinna* make exploratory excursions farther from their home ranges than the other species, and they tend to be found in foraging assemblages dominated by roaming fishes, such as parrotfishes (Family Scaridae), or goatfishes (Family Mullidae) as juveniles. This behaviour increases as they get larger.

Establishment of activity centers within the home range areas

For the labrid species in this study, activities were found to be non-randomly distributed within the home range. The 50% core use areas or activity centers covered only 13-26% of the total home range areas. This finding agrees with other studies that investigated activity centers within home range areas of other fish species. Nursall (1977) studied territoriality in redlip blennies, *Ophioblennius atlanticus* (Family Blennidae), and estimated that it spends about 99% of its time within about 50% of its territory, and about 80% of its time within about 5% of its territory. For the same species, Osburn (1972) described short bursts of feeding activity from a particular station within a stable home range. Bradbury et al. (1995) reported that female cunner, *Tautoglabrus adspersus* (Labridae) used space disproportionately within their home range boundaries by spending 60% of the time in 24-32% of their home range area. Chilton and Poarch (1997) looked at movement in a freshwater species, the grass carp, *Ctenopharyngodon idella* (Family Cyprinidae) and found that the 50% core use area encompassed 5.2 km², while the 95% home range area encompassed 32.3km², which means that 50% of observation points were observed in approximately 16% of the home range area. Freeman and Alevizon (1983) studied the coral reef fish, *Gramma loreto* (Family Grammatidae) and found that although this species occupies a home range area of 0.2-1.2 m², it defends only a portion of this area (approximately 0.03-0.87m², or 15-73%). The labrids in this study did not appear to actively defend their core use areas, although social interactions may have a large influence on the core use size and position (Chapter IV and VI).

Other studies have found that specific behaviours are non-randomly distributed throughout the home range area. Coleman and Wilson (1996) found that juvenile pumpkinseed sunfish (*Lepomis gibbosus*, Family Centrarchidae) had a higher feeding rate in the center of their home range than on the periphery. Cole (1984) found that areas of activity were characterized primarily

by aggressive feeding, and station maintenance (i.e. sitting on the substrate, under cover, or perching on a rock) events in the temperate marine goby, *Coryphopterus nicholsii* (Family Gobiidae). Aggressive events occurred mainly on the periphery of areas of activity, while feeding occurred both peripherally and centrally. Typically, she observed individuals perched on a rock or resting on the substrate in a central location, and from there, they would make short, rapid excursions out towards the perimeter, either to feed or to attack an intruder (Cole 1984). The distribution of specific behaviours within the home range areas may reveal similar results for the labrid species in this study (Chapter IV).

Concluding statements

It is important to acquire a better understanding of home range requirements in animals because humans are perpetually taking over or impacting “natural” spaces. The aquatic realm is not immune to such events. By studying space use and requirements in reef fish species, we may be able to manage populations and communities more effectively. For example, Kramer and Chapman (1999) point out that in small marine reserves, a significant proportion of fish whose home ranges are centered within the reserve can still be exposed to fishing mortality because their home ranges include non-reserve areas. Acquiring better information on space use and patterns of movement of fishes within the marine reserve would provide stronger arguments for establishing larger no-take boundaries.

In this study, different estimates of home range area were acquired from the two methods of calculation (AK and MCP). The advantages and disadvantages of these two methods were briefly discussed, but the effects of these two methods on the results demonstrated a need for other researchers to be prudent in reporting the methods used to calculate home range area. This would result in greater validity of cross-study comparisons for home range size estimates.

Finally, for all species in this study, despite the strong correlations between fish size and

home range area, there are other factors that may affect home range size such as microhabitat availability, topographical features, or the configuration of neighbours. These factors may also affect the location of the activity centers within the home range area. Future studies will investigate these factors on the position, size, and shape of the activity centers and total home range area.

Table 2.1. Home range area estimates for numerous reef fishes. Data were collected from various sources (Sale 1978a, Kramer and Chapman 1999). The home range radii for additional species are listed in Smith and Tyler (1972). Nocturnal species are denoted with a letter N, although their diurnal space use is reported. Temperate reef species are denoted by T, and those species names not followed by a letter are tropical coral reef species.

Family Genus and Species	Fork Length (mm)	Home Range Area (m ²)	Reference
Acanthuridae <i>Acanthurus achilles</i> <i>A. lineatus</i> <i>A. nigrofasciatus</i>	? 240 (TL) ¹ ? 380 (TL) ¹ ? 210 (TL) ¹	5-20 4-12.5 5-20	Barlow (1974a) Nursall (1974) Barlow (1974a)
Apogonidae <i>Apogon townsendi</i> (N) <i>A. lachneri</i> (N) <i>A. phenax</i> (N)	30-55 30-55 30-65	0.2 0.5 0.2	Luckhurst and Luckhurst (1978) Luckhurst and Luckhurst (1978) Luckhurst and Luckhurst (1978)
Blenniidae <i>Ophioblennius atlanticus</i>	44-70	0.2-1.7	Nursall (1977)
Chaetodontidae <i>Chaetodon unimaculatus</i>	? 200 (TL) ¹	< 314	Reese (1973)
Cheilodactylidae <i>Cheilodactylus fuscus</i> (T)	284	3639	Lowry and Suthers (1998)
Cirrhitidae <i>Amblycirrhitus pinos</i>	25-65	2.5	Luckhurst and Luckhurst (1978)
Clinidae <i>Acanthemblemaria spinosa</i> <i>Emblemaria bahamensis</i>	20-30 20-30	0.03 0.03	Luckhurst and Luckhurst (1978) Luckhurst and Luckhurst (1978)
Gobiidae <i>Priolepis hipoliti</i>	15-35	0.5	Luckhurst and Luckhurst (1978)
Grammatidae <i>Gramma loreto</i> <i>G. loreto</i> <i>Lipogramma trilineata</i>	20-60 40-60 15-35	0.5 0.2-1.2 0.8	Luckhurst and Luckhurst (1978) Freeman and Alevizon (1983) Luckhurst and Luckhurst (1978)
Holocentridae <i>Holocentrus marianus</i> (N) <i>Myripristis jacobus</i> (N) <i>Plectropops retrospinus</i> (N)	80-150 90-140 50-100	1.1 3.1 1.1	Luckhurst and Luckhurst (1978) Luckhurst and Luckhurst (1978) Luckhurst and Luckhurst (1978)
Labridae <i>Bodianus rufus</i> <i>Halichoeres bivittatus</i> <i>H. garnoti</i> <i>H. maculipinna</i>	190 114 (TL) 119 (TL) 117 (TL)	190 114 (TL) 119 (TL) 117 (TL)	Hoffman (1983) adults only, this study adults only, this study adults only, this study

Table 2.1 (Continued)			
Family Genus and Species	Fork Length (mm)	Home Range Area (m ²)	Reference
Labridae (continued)			
<i>Halichoeres poeyi</i>	107 (TL)	26.5	adults only, this study
<i>Notolabrus fucicola</i> (T)	500 max	>1750	Barrett (1995)
<i>N. tetricus</i> (T)	450 max	225-775	Barrett (1995)
<i>Pictilabrus laticlavius</i> (T)	300 max	175	Barrett (1995)
<i>Pseudolabrus psittaculus</i> (T)	250 max	280-375	Barrett (1995)
<i>Thalassoma bifasciatum</i>	74 (TL)	33.2	adults only, this study
<i>T. bifasciatum</i>	n/a	45	Fitch and Shapiro (1990)
Monacanthidae			
<i>Meuschenia australis</i> (T)	300 max	> 1750	Barrett (1995)
Pomacanthidae			
<i>Centropyge argi</i>	38-64	1.1	Luckhurst and Luckhurst (1978)
Pomacentridae			
<i>Stegastes biocellatus</i>	76	3.1	Keenleyside (1972)
<i>Dascyllus aruanus</i>	40	3	Sale (1971)
<i>Eupomacentrus rectifraenum</i>	≤120	2	Montgomery (1980)
<i>Microspathodon dorsalis</i>	≤220	0.5	Montgomery (1980)
<i>Parma victoriae</i>	93-96	3-26	Norman and Jones (1984)
<i>Pomacentrus flavicauda</i>	66	2	Low (1971)
<i>P. flavicauda</i>	? 90 (TL) ¹	2	Reese (1973)
<i>Stegastes dienaecus</i>	70-110	3.1	Luckhurst and Luckhurst (1978)
<i>S. dorsopunicans</i>	138	2.1	Ferreira et al. (1998)
<i>S. partitus</i>	50-80	4.5	Luckhurst and Luckhurst (1978)
<i>S. planifrons</i>	50-100	2.5	Luckhurst and Luckhurst (1978)
Priacanthidae			
<i>Priacanthus cruentatus</i> (N)	150-250	1.8	Luckhurst and Luckhurst (1978)
Scaridae			
<i>Sparisoma viride</i>	280	497	van Rooij et al. (1996)
Sciaenidae			
<i>Equetus punctatus</i> (N)	140	3.1	Luckhurst and Luckhurst (1978)
Serranidae			
<i>Epinephelus guttatus</i>	254	862	Shapiro et al. (1994)
<i>Hypoplectrus spp.</i>	50-100	150-200	Barlow (1975)
<i>Liopropoma carmabi</i>	25-40	0.8	Luckhurst and Luckhurst (1978)
<i>L. mowbrayi</i>	35-65	1.8	Luckhurst and Luckhurst (1978)
<i>L. rubre</i>	35-65	1.8	Luckhurst and Luckhurst (1978)
<i>Plectropomus leopardus</i>	490	10458	Zeller (1997)
<i>P. leopardus</i>	330-660	2000	Samoilys (1997)
Syngnathidae			
<i>Micrognathus ensenadae</i>	90-200	5.3	Luckhurst and Luckhurst (1978)
Tetraodontidae			
<i>Canthigaster rostrata</i>	53	20	Sikkel (1990)

Family Genus and Species	Fork Length (mm)	Home Range Area (m ²)	Reference
Tripterygiidae <i>Enneanectes atrorus</i> <i>Forsterygion varium</i>	15-30 75-100	0.13 1.5-2.0	Luckhurst and Luckhurst (1978) Thompson (1983)

¹The numbers presented are maximum length estimates from Froese and Pauly (1999).

Table 2.2. Linear regression analyses of \log_{10} AK 95% home range area (m^2) against \log_{10} total length (cm).

SPECIES	n	a	b	r^2	p
<i>Halichoeres bivittatus</i>	77	1.64	-0.25	0.9	< 0.001
<i>H. garnoti</i>	23	2.01	-0.71	0.64	< 0.001
<i>H. maculipinna</i>	26	1.14	0.38	0.44	< 0.001
<i>H. poeyi</i>	26	1.69	-0.44	0.4	< 0.001
<i>H. radiatus</i>	11	2.26	-0.96	0.53	0.007
<i>Thalassoma bifasciatum</i>	24	1.78	-0.094	0.61	< 0.001

Table 2.3. Combined home range area data for *Halichoeres bivittatus*, *H. garnoti*, and *Thalassoma bifasciatum*. This table shows the results of linear regression analyses on \log_{10} home range area (m^2) against \log_{10} fish length (cm) for all three species pooled. Home range size was calculated using the Adaptive Kernel method, and only the 95% utilization distribution is analysed here.

Regression	n	a	b	r^2	p
juveniles + initial phase adults	124	1.54	-0.15	0.74	< 0.001
juveniles	57	0.77	0.24	0.19	< 0.001
initial phase adults	67	0.29	1.19	0.0092	0.208

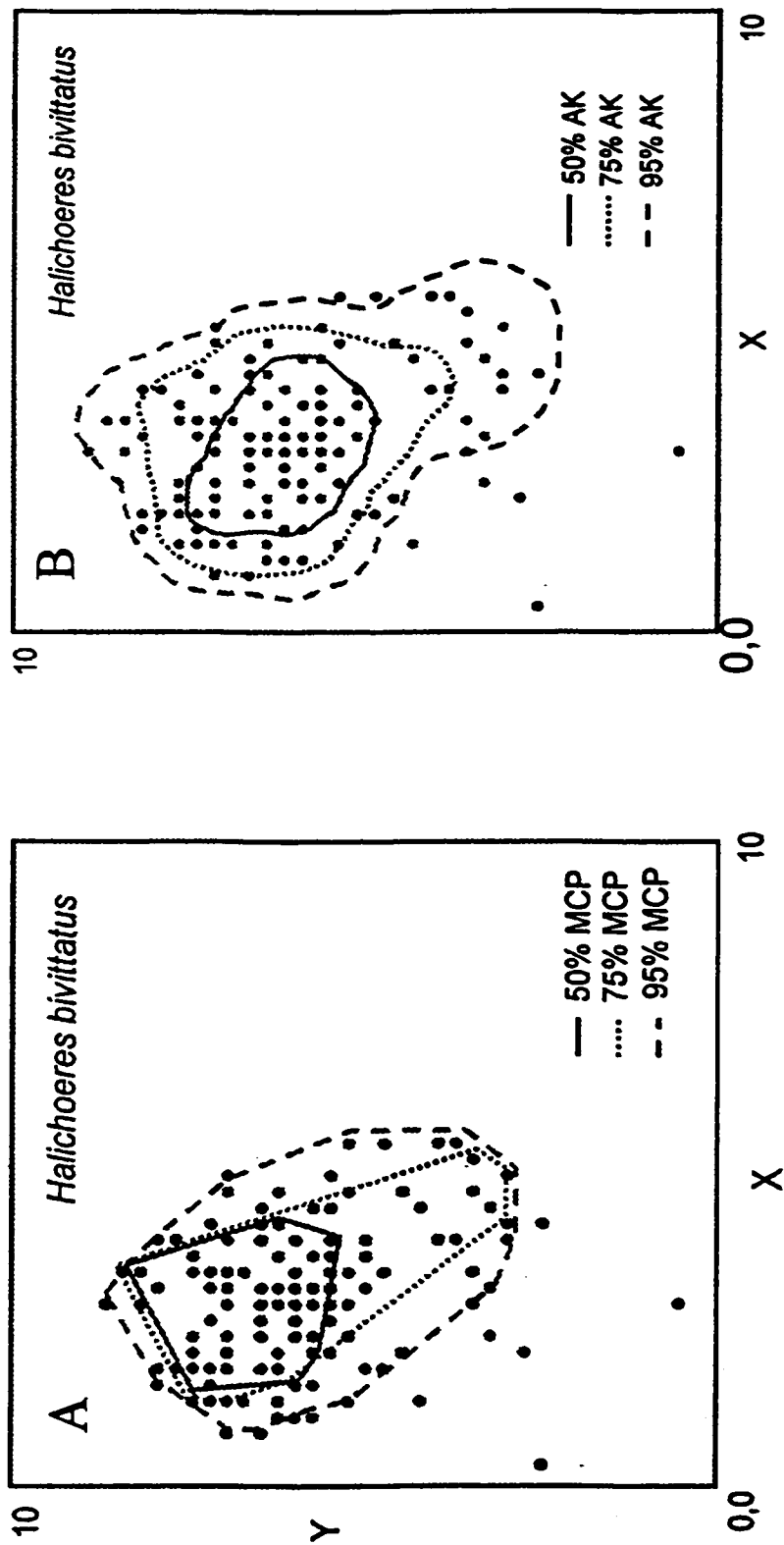


Figure 2.1. Examples of point percentage contour calculations for an adult *Halichoeres bivittatus*. Figure A was constructed using the Minimum Convex Polygon (MCP) method, and Figure B was constructed using the Adaptive Kernel (AK) method. The 50% contour denotes the core use area in this study. Note that the isopleth areas (or the areas between the contours) are generally smaller using the MCP method compared with the AK method. The scale on the axes is in meters.

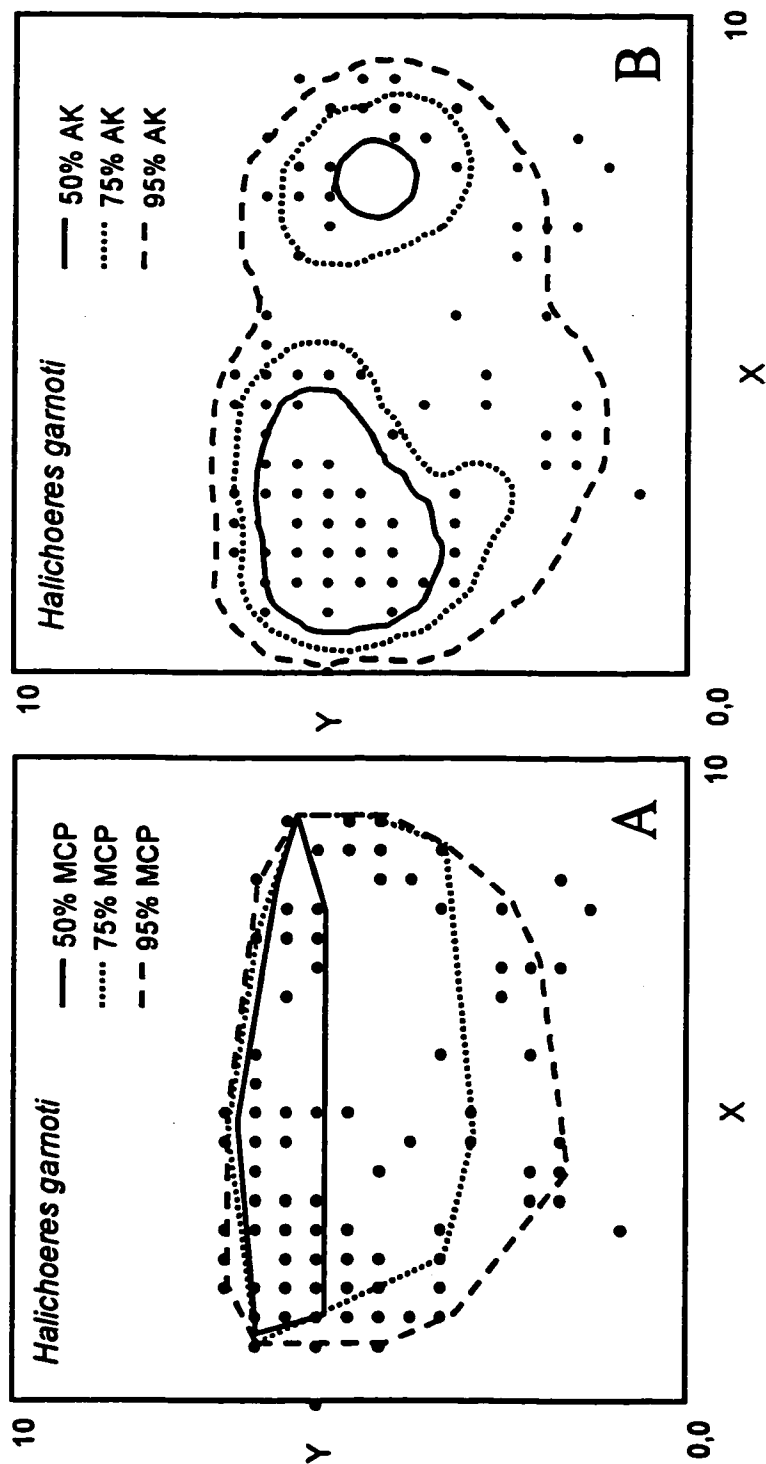


Figure 2.2. Examples of point percentage contour calculations for an adult *Halichoeres garnoti*. Figure A was constructed using the Minimum Convex Polygon (MCP) method, and Figure B was constructed using the Adaptive Kernel (AK) method. Note that the MCP method delineates only one core use area (the 50% contour), whereas the AK method delineates two core use areas. The scale on the axes is in meters.

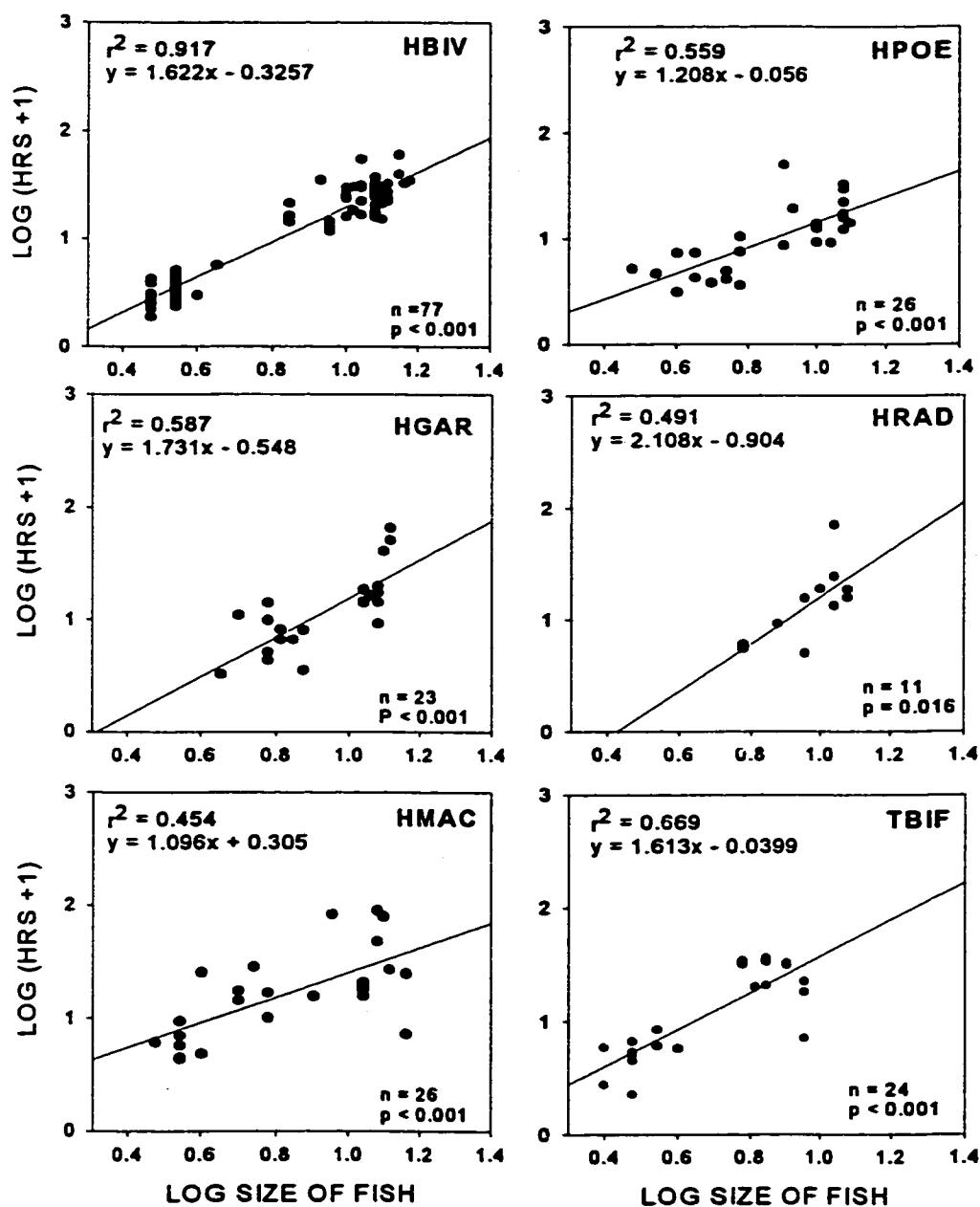


Figure 2.3. Positive relationship of increasing home range size (HRS) with fish size. Home range size was calculated using the Minimum Convex Polygon method, and only the 95% point percentage contour is plotted. To improve normality and homogeneity of variances, home range area (m^2) and fish size (total length in cm) were \log_{10} transformed prior to analysis. Each species is shown separately: HBIV = *Halichoeres bivittatus*, HPOE = *H. poeyi*, HGAR = *H. garnoti*, HRAD = *H. radiatus*, HMAc = *H. maculatus*, and TBIF = *Thalassoma bifasciatum*.

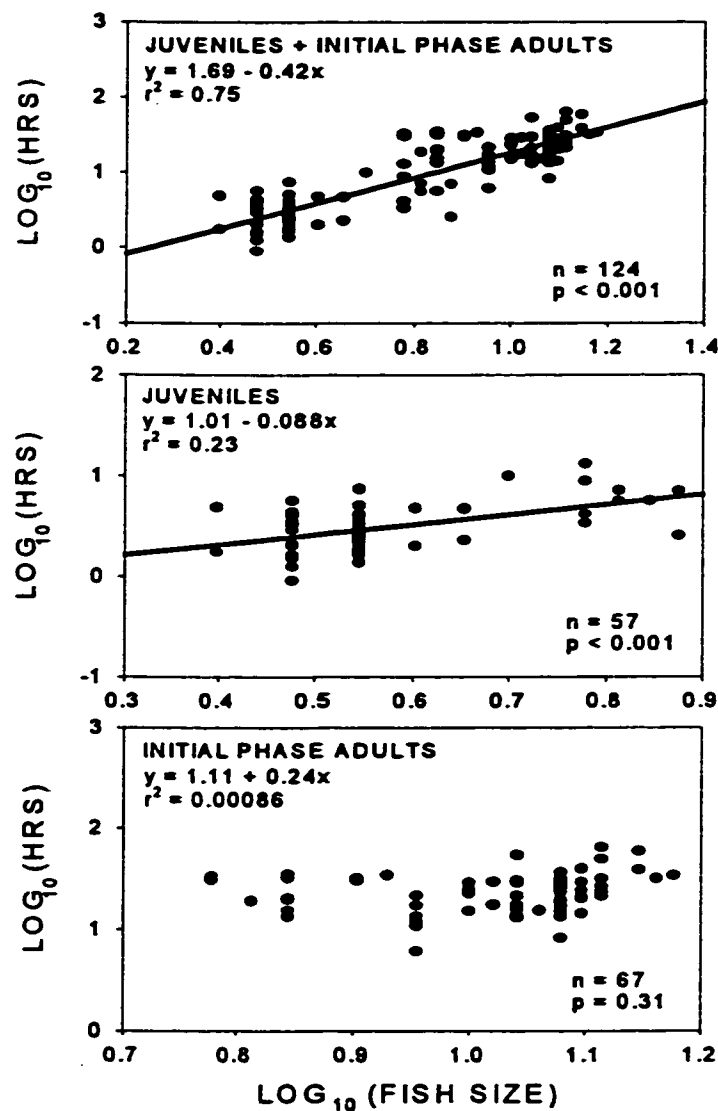


Figure 2.4. Combined home range size (HRS) data for *Halichoeres bivittatus*, *H. garnoti*, and *Thalassoma bifasciatum*. These figures show \log_{10} home range size vs. \log_{10} fish size for all three species pooled. Home range size was calculated using the Minimum Convex Polygon method, and only the 95% utilization distribution is plotted. There is a significant relationship for juveniles + initial phase adults, for juveniles alone, but not for initial phase adults alone. This third figure may represent a plateau in home range size once the status of initial phase is reached.

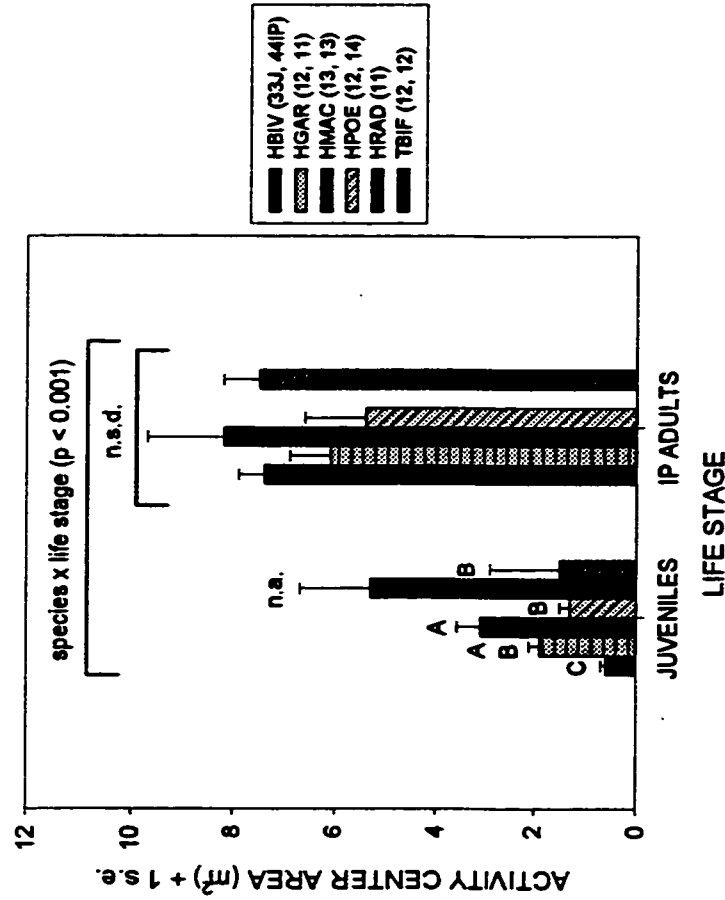


Figure 2.5. Average core use area estimates for the six labrid species (estimated from the 50% AK utilization distribution). The letters above the bars show results from Tukey's *post hoc* tests that followed a 2-way ANOVA on \log_{10} AK50% core use area estimates. Common letters above the bars indicate no significant difference at $p < 0.05$. Within a species, IP adults always had larger core use areas than juveniles ($p < 0.05$). There was a significant species x life stage interaction ($p < 0.001$), which indicates that the rate of core use area increase between juveniles and adults depends on the species. n.a. = not analysed; n.s.d. = not significantly different (i.e. $p > 0.05$). HBIV = *Halichoeres bivittatus*, HGAR = *H. garnoti*, HMAc = *H. maculipinna*, HPOE = *H. poeyi*, HRAD = *H. radiatus*, and TBIF = *Thalassoma bifasciatum*.

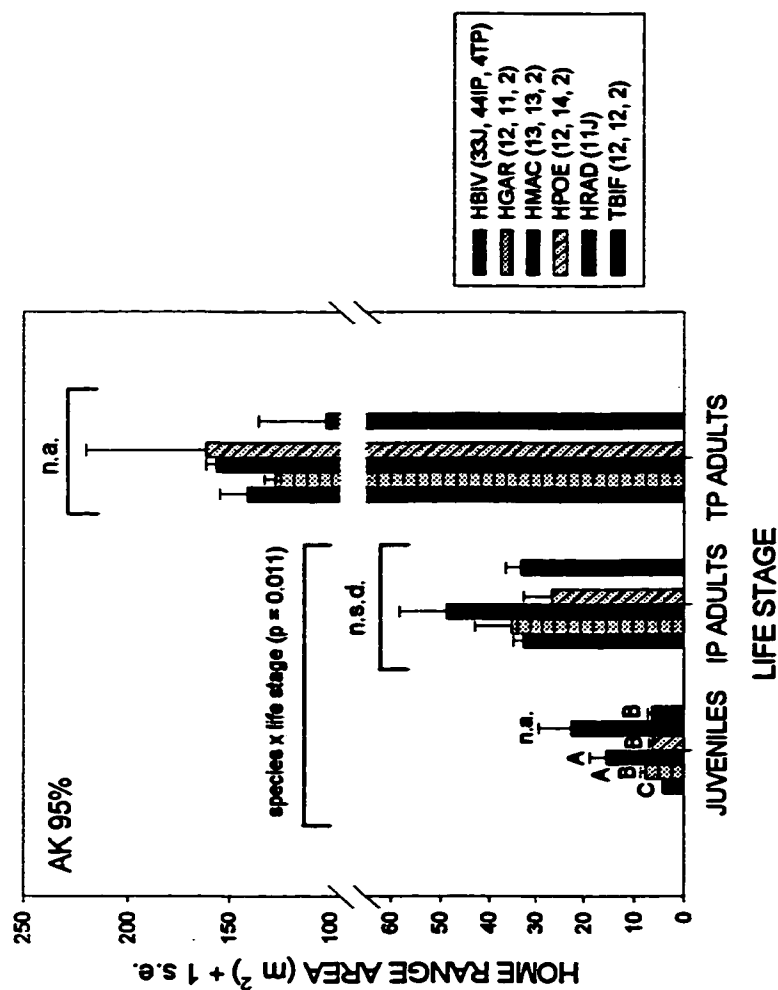


Figure 2.6. Average home range area estimates for the six labrid species (estimated from the 95% AK utilization distribution for juveniles and IP adults, see methods for TP procedures). The letters above the bars show results from Tukey's *post hoc* tests that followed a 2-way ANOVA on \log_{10} AK95% home range area estimates. Common letters above the bars indicate no significant difference at $p < 0.05$. Within a species, IP adults always had larger home ranges than juveniles ($p < 0.05$). There was a significant species x life stage interaction ($p = 0.011$), which indicates that the rate of core use area increase between juveniles and adults depends on the species. n.a. = not analysed; n.s.d. = not significantly different (i.e. $p > 0.05$). HBIV = *Halichoeres bivittatus*, HGAR = *H. garnoti*, HMAc = *H. maculipinna*, HPOE = *H. poeyi*, HRAD = *H. radiatus*, and TBIF = *Thalassoma bifasciatum*.

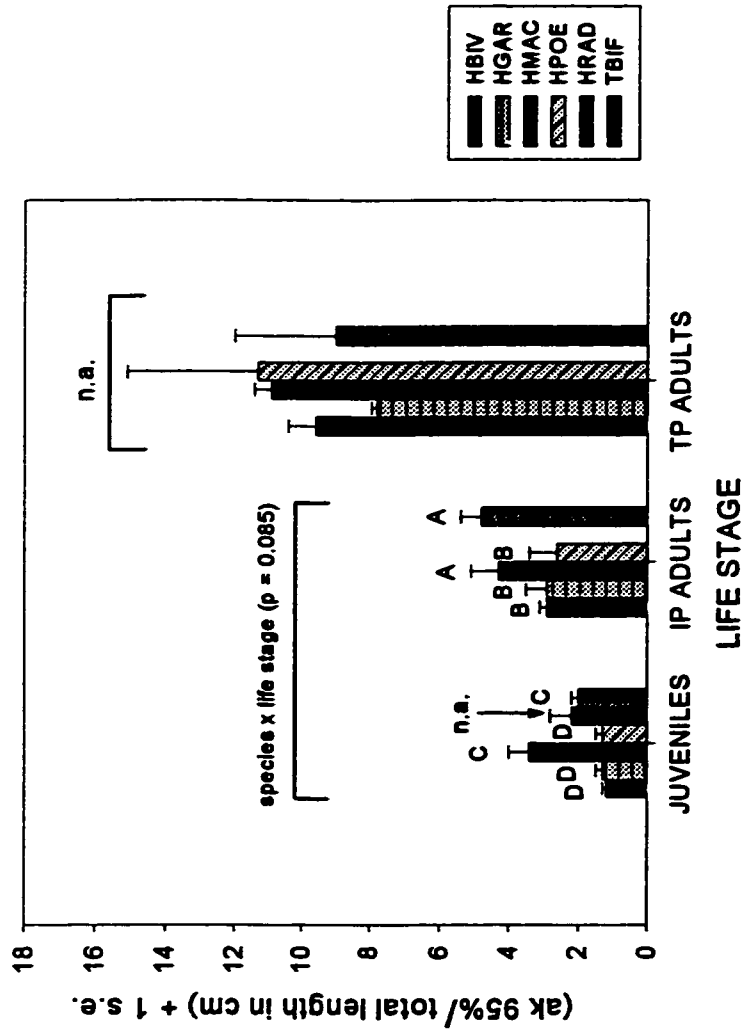


Figure 2.7. Area requirements per centimeter of fish length. The letters above the bars show results from Tukey's *post hoc* tests that followed a 2-way ANOVA on \log_{10} (AK95% / total length) data. Common letters above the bars indicate no significant difference at $p < 0.05$. Within a species, IP adults always had larger area requirements per centimeter of fish length than juveniles ($p < 0.05$). Although not analysed, TP adults appear to have much larger area requirements per cm of fish length. There was no significant interaction between species X life stage ($p = 0.085$). n.a. = not analysed; sample sizes are those listed in Fig. 2.6.

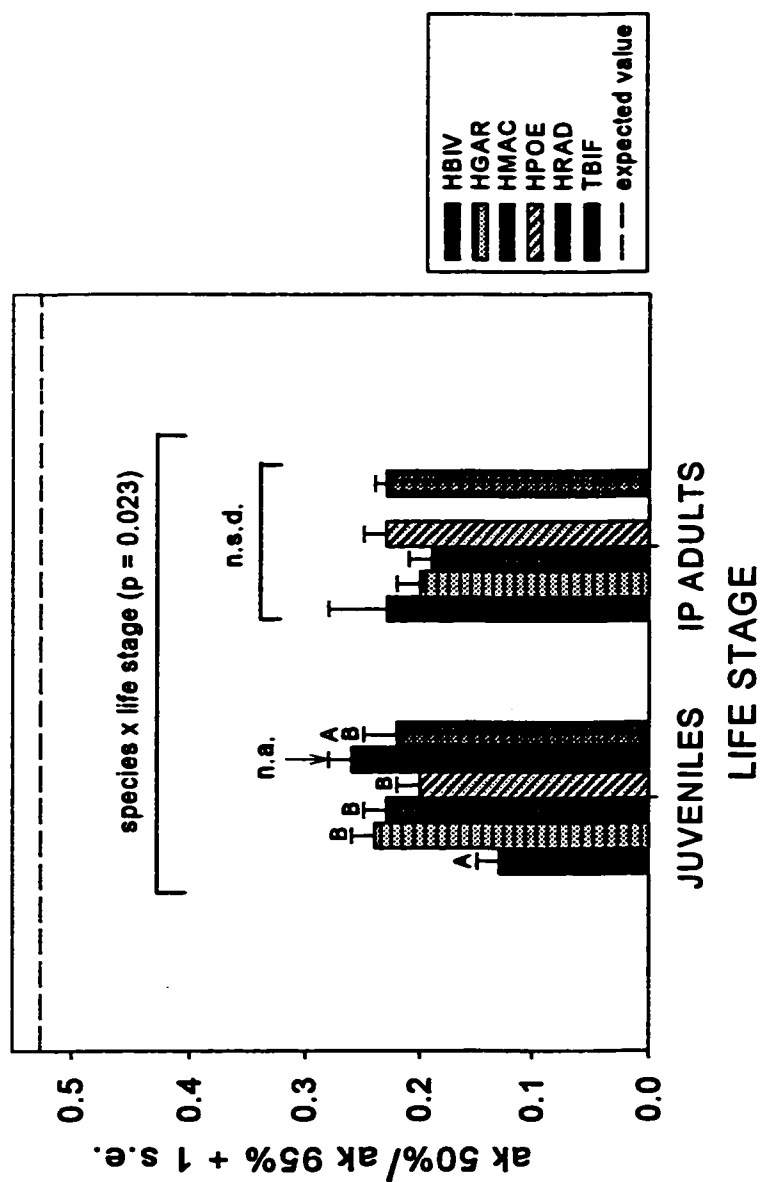


Figure 2.8. Relative area coverage of the core use area (calculated by dividing AK 50% m^2 / AK 95% m^2). The dashed line represents the expected proportion coverage of area by the 50% utilization distribution. The letters above the bars show results from Tukey's *post hoc* tests that followed a 2-way ANOVA on angular transformed AK50% / AK 95% home range area estimates. Common letters above the bars indicate no significant difference at $p < 0.05$. There was a significant species x life stage interaction ($p = 0.023$). n.a. = not analysed, n.s.d. = not significantly different; sample sizes are those listed in Fig. 2.5.

CHAPTER III

BEHAVIOURAL OVERLAP IN SIX CARIBBEAN LABRID SPECIES: INTRA- AND INTER- SPECIFIC SIMILARITIES

ABSTRACT

This study investigates behavioural similarities in six ecologically and morphologically similar labrid species. Ontogenetic shifts in behaviour within species are also considered. There have been many studies on ontogenetic differences in fish with respect to diet, microhabitat use, and visual acuity and how it pertains to foraging ability; however, fewer studies have been specifically directed towards the ontogeny of behaviours. Initially, I recorded five- minute behavioural observations of randomly chosen juvenile and initial phase adults from each of the following species: *Halichoeres bivittatus*, *H. garnoti*, *H. maculipinna*, *H. poeyi*, *Thalassoma bifasciatum*. Only juvenile *H. radiatus* were observed. The behaviours recorded were general categories, which resulted in a high degree of overlap among the species and life stages (Discriminant Function Analysis (DFA) correctly classified only 20% of the individuals).

In a second phase of this study, I recorded more detailed observations (18 categories) to better discriminate among species and life stages. The observation periods lasted 10 minutes, and four periods per individual were pooled for analysis. The same species and life stages used in the initial study were included, with the addition of terminal phase adults for all species except *H. radiatus*. These observations yielded more conclusive results, although there was still a high degree of overlap among species and life stages (DFA correctly classified 60% of the individuals). Species were separated in the first discriminant function by an inverse relationship between the

frequency of “hiding” (= out of view) and eating, and life stages were separated in the second discriminant function by an inverse relationship between the frequency of swimming alone and “eye flickering” (= remaining motionless and twitching their eyes). Eye flickering is assumed to be a behavior that increases an individual’s awareness of predators or environmental threats. Notable differences among species included the greater frequencies of hiding by juvenile *H. radiatus*, and all life stages of *H. garnoti*. As all these labrids grow, they increase their frequencies of swimming alone, and decrease their frequencies of hovering and searching for food. There was a remarkable similarity in ontogenetic changes in these behaviours for all of the species studied.

INTRODUCTION

Behavioural investigations can reveal many aspects of social interactions and spatial dynamics (space use and movement) in animal systems. Coral reef fish assemblages are highly diverse, complex systems that are accessible and directly observable for this purpose. This study investigates behavioural similarities among ecologically and morphologically similar labrids, including: *Halichoeres bivittatus*, *H. garnoti*, *H. maculipinna*, *H. poeyi*, *H. radiatus*, and *Thalassoma bifasciatum*. While much is known for these species with respect to diet (Randall 1967, Anonymous 1969, Roede 1972, Wainwright 1988), ecology (Bohlke and Chaplin 1968, Roede 1972, Thresher 1979, Robertson 1981), taxonomy (Randall and Bohlke 1965, Bohlke and Chaplin 1968, Roede 1972), and details of sexual development (protogynous hermaphroditism) and their social mating systems (Feddern 1965, Reinboth 1973, Warner 1975, Warner et al. 1975, Warner and Robertson 1978, Warner and Hoffman 1980a,b, Robertson 1981, Fitch and Shapiro 1990), little is known about daily time budgets of behaviour and how they differ among juveniles, initial phase, and terminal phase adults.

The labrids in this study are demersal, highly gregarious, and readily form heterospecific

groups. They are predominantly carnivorous, yet highly opportunistic, and frequently pick food from sand, algal turf, corals and rocks (Roede 1972). The *Halichoeres* species consume a wide variety of benthic organisms, including shelled invertebrates, crustaceans, and worms.

Thalassoma bifasciatum is also a generalist feeder, but eats zooplankton and cleans ectoparasites from other fish (Feddern 1965, Randall 1967). There is high overlap among diets of these species. Despite this, these species show limited aggression among conspecifics and heterospecifics (*pers. obs.*, Fitch and Shapiro 1990), which suggests minimal levels of competition among them. This study investigates the extent of behavioural similarities which is an essential part of exploring their ability to coexist.

Ontogenetic shifts have been documented for many fish species with respect to diet and resources (Werner and Gilliam 1984, Bellwood 1988, Harmelin-Vivien 1989, Holbrook et al. 1990, Malmquist et al. 1992, Wu and Culver 1992, Muñoz and Ojeda 1998, Garcia Berthou 1999a, Hoines and Bergstad 1999, Platell and Potter 1999), and microhabitat (Stoner 1983, Shulman and Ogden 1987, Harmelin-Vivien 1989, Sogard et al. 1989, L'Abée Lund et al. 1993, Sayer et al. 1993, Lirman 1994, Eggleston 1995, Allen and Baltz 1997, Molls 1999). In freshwater fish, it is actually the exception when age classes fail to show much separation in diets (Keast 1977, Keast 1978, Werner and Gilliam 1984, Gerking 1994, Helfman 1994, Matthews 1998). Indeed, virtually all freshwater fish and many marine fish pass through a plankton-feeding stage during ontogeny (Winfield 1991). Ontogenetic shifts in diet, behaviour, and microhabitat complicate our ability to place fish species into functional groups, because a species' role in an assemblage will change with growth (Matthews 1998). It is critical for fish conservationists to understand ontogenetic shifts in order to effectively manage the various life history stages.

Commonly, ontogenetic dietary shifts are coupled with microhabitat shifts (Jones 1984a, Werner and Gilliam 1984, Mittelbach and Osenberg 1993, Setran and Behrens 1993, Hyndes et al.

1997, Garcia Berthou 1999b). In a typical example, juvenile *Pseudolabrus celidotus* (Labridae) are closely associated with macroalgal shelter, but their shelter-dependence appears to decrease with growth (Jones 1984a). At the same time, they switch from feeding on micro-crustaceans present in macroalgae to those associated with bare rock-coralline turf areas, where the adults are found. Another typical example is the obligatory shift in microhabitat when fishes shift from feeding on zooplankton to feeding on benthic invertebrates or other fishes (e.g. Werner and Gilliam 1984, Mittelbach and Osenberg 1993, Garcia Berthou 1999b). Ontogenetic habitat shifts can often facilitate the partitioning of food resources between conspecifics or among similar species (Hyndes et al. 1997).

While studies in ontogenetic shifts in diet and microhabitat in fishes are rather common, studies that focus on ontogenetic shifts in behaviour beyond the early life history stages (e.g. embryonic and larval stages) are relatively rare (for a recent review, see Skúlason and Smith 1995). Ontogenetic shifts in behaviour have been recorded for embryo-larva-juvenile morphological stages in the shortnose sturgeon (*Acipenser brevirostrum*, Acipenseridae) with respect to phototaxis, rheotaxis, and their attachment to shelter (Richmond and Kynard 1995). Several studies have found simultaneous ontogenetic shifts in behaviour and microhabitat (Stein et al. 1992, Lowe et al. 1996, Lawson et al. 1999). Small juvenile pygmy rockfish, *Sebastes wilsoni* (Scorpaenidae), form dense schools above shallower rocky ridges than larger individuals that occur in nonpolarized assemblages on the bottom in cobble and boulder fields (Stein et al. 1992). In contrast, schooling behaviour in two Caribbean surgeonfishes (*Acanthurus coeruleus* and *A. bahianus*) occurs primarily in adults, and small juveniles never participate in the large, dense, roaming schools (Lawson et al. 1999). Diet, behaviour and habitat shifts have also been observed in the tiger shark, *Galeocerdo cuvier* (Carcharinidae), as it matures (Lowe et al. 1996). Smaller sharks are spatially segregated from larger sharks and appear to be primarily nocturnal, bottom

feeders. Larger sharks are highly opportunistic and feed near the bottom at night and at the surface during the day. Lockett and Suthers (1998) found a similar degree of change in diet, foraging behaviour, and habitat in the temperate reef fish, *Cheilodactylus fuscus* (Cheilodactylidae). Juveniles occur in turf algae in the upper subtidal regions and feed continuously throughout the day. Adults consume significantly greater proportions of brachyurans, molluscs, and echinoderms than juveniles, they occur in deeper subtidal habitats, and rarely feed during the day. Ontogenetic changes in foraging behaviour and prey selection have also been observed in the labrid, *Coris gaimard* (Shibuno et al. 1994). Interestingly, both the size of gravel turned over and the relative frequency of gravel turning increase as this labrid grows. In another intriguing study that investigated ontogenetic changes in behaviour, Sakakura and Tsukamoto (1999) found that in the migratory yellowtail, *Seriola quinqueradiata* (Carangidae), the onset of aggressive behaviour occurs just after metamorphosis into juveniles, and coincides with a significant increase in tissue cortisol levels. In contrast, Gomelyuk and Leunov (1999) found that smaller greenlings (Hexagrammidae) appear to be sedentary and exhibit a higher incidence of agonistic behaviour than older, larger individuals.

This study investigates behaviour and social interactions in three life stages (juveniles, initial phase and terminal phase adults) of several ecologically and morphologically similar labrid species. First, I wanted to identify important behaviours in their daily time budgets. Second, I wanted to determine if I could predict group membership (species and life stages) based on the behaviours recorded. The questions addressed in this study include: 1) Are there behaviours that separate the species? 2) Are there behaviours that separate life stages? and 3) Do these species go through similar ontogenetic shifts in behaviour as they mature?

METHODS

Study sites

This study occurred on the barrier reef of Tague Bay, St. Croix, U.S.V.I. (17° 36'N, 64° 36'W). Behavioural observations were recorded while on SCUBA or snorkel over reef habitat between 2 and 10 m deep. The five-minute behavioural observations were performed on randomly chosen fish while swimming along continuous reef stretches of fore and back reef habitats of Tague Bay during May-August 1997. The more detailed approach, with four sets of 10-minute observations, was part of a corollary study on home range requirements (Chapter II). This study occurred during May-August of 1998 and 1999 along back reef areas.

Study animals

Juveniles, initial phase (IP), and terminal phase (TP) adults of the following labrid species were studied: *Halichoeres bivittatus*, *H. garnoti*, *H. maculipinna*, *H. poeyi*, *Thalassoma bifasciatum*. *Halichoeres radiatus* juveniles were included, but adults are much larger and more mobile than the other life stages and species so they were excluded from this study. There is considerable difference in color among these labrids as well as among the life stages within species. Colour pattern often provided good indication of life stage within these species (Roede 1972, Warner and Robertson 1978). Juveniles and IP adults are easily distinguishable for *H. garnoti* and *H. radiatus*. For *H. bivittatus*, *H. maculipinna*, *H. poeyi*, and *Thalassoma bifasciatum* juveniles were ≤ 30 mm in total length (*c.f.* Warner and Robertson 1978). Terminal phase individuals were easily distinguished from IP and juveniles in all of the species because of their bolder colour patterns (except *Halichoeres poeyi*), and changes in morphology.

Behavioural study I: 5 -minute observations

This preliminary study investigated general behavioural differences between juveniles and IP adults within species, and behavioural differences among species. Prior to collecting data on

individuals, a randomized order of species and life stages was preset on an underwater slate. As individuals that fulfilled the criteria were encountered while SCUBA diving along continuous back- and fore- reef habitat, I began behavioural observations after two minutes of following the fish (to allow for acclimation). If the required individual was not found within 3 minutes of searching, I went on to the next individual in the list. I followed each individual for five minutes, and recorded behaviours every 10 seconds, for a total of 30 observations per individual. Behaviours included: eating (= biting at the surface or jaw movements), swimming alone, swimming with others (either conspecifics or heterospecifics), aggression (either as the aggressor, or the one being chased), hiding (= out of view), and any other behaviours were combined into a separate category. From May until August 1997, I recorded the behaviours of 252 labrids using these methods (juvenile *Halichoeres radiatus*, n = 13; juveniles and IP adults for *H. bivittatus*, n = 15, 14, respectively; *H. garnoti*, n = 31, 32; *H. maculipinna*, n = 26, 31; *H. poeyi*, n = 11, 14; and *Thalassoma bifasciatum*, n = 32, 33). *Halichoeres bivittatus* and *H. poeyi* are rare on the fore reef of Tague Bay, so they have smaller sample sizes.

Behavioural study II: 4 sets of 10-minute observations

The preliminary study provided a “snapshot” of general labrid behaviours. I was interested in determining if group membership could be better predicted by refining the behaviours observed, and by following individuals repeatedly over a longer time. During the preliminary study, I also made qualitative observations of behavioural differences between IP and TP individuals, so I decided to include TP adults in this more detailed study. This study included juvenile *Halichoeres radiatus*, and juveniles, IP and TP adults for the other five species. Earlier studies of the bluehead wrasse, *Thalassoma bifasciatum*, have shown it to be a migratory spawner with large terminal-phase males defending temporary spawning territories (Warner 1975, Warner et al. 1975, Warner and Robertson 1978). However, Fitch and Shapiro (1990) describe a different

social structure where fish occupy permanent home ranges, spawn within or near these home ranges, and are not territorial. Only *T. bifasciatum* that demonstrated long-term site fidelity were included in this study.

Initially in 1998, individual fishes of all species were caught with a lift net (see Roede 1972) and tagged with beaded Floy® tags to verify the sedentary nature of these labrids. The fishes were anaesthetized with clove oil prior to tagging (Munday and Wilson 1997). The fishes quickly regained consciousness and resumed normal behaviours. After these preliminary investigations, I found that individual labrids could be reliably identified without catching and tagging by recognizing differences in facial markings, lateral line deformities, and/or size differences.

Quadrats (10x10 m²) were haphazardly marked on the reef with flagging tape. The habitat features of each quadrat were mapped on a slate. Mylar film was then placed over the map to record the positions of an individual fish during each observation period. Observations occurred between 0800 hr and 1500 hr, which appeared to be the peak activity periods for labrids on the reef. Observation periods were aborted if the focal individual was involved in a spawning episode (which often occurs outside of the normal home range area). Observations were also not carried out on days when visibility fell below 10m (during storm events or algal blooms), because the fish were behaving abnormally. Individual fishes were randomly selected from each quadrat for observation. Each observation period lasted for 10 minutes, and at every 20 second interval, several aspects about the position (microhabitat use, swimming distance above the substrate), social interactions, and the behaviour of that fish was recorded (for a total of 30 points per observation period). The observation periods were pooled for each individual to get a better assessment of daily activities (the time of day was randomized for repeated observations). In a preliminary study, I found that an additional set of observations did not affect the size of the home

range area estimated from four sets (Mann Whitney $T = 986.00$; $p = 0.812$). Thus, only four sets of observations were conducted on all subsequent focal individuals. The spatial coordinates were analysed in a separate study on home range (Chapter II). Microhabitat was analysed in a separate study (Chapter V).

The following behaviours were quantified: 1) eating/Biting at the substrate (= “strike” (Aronson and Sanderson 1987)); 2) touching substrate with nose; 3) swimming alone, 4) swimming with conspecifics; 5) swimming with heterospecifics; 6) swimming with conspecifics and heterospecifics; 7) being chased by damselfish (= “flee” (Aronson and Sanderson 1987); aggressive acts by damselfish are characterized by chasing and biting, and the focal labrid typically swam away (Shulman 1985, Fitch and Shapiro 1990, Itzkowitz 1990)); 8) chasing or fighting with another individual (= “chase” (Aronson and Sanderson 1987)); 9) looking at substrate (= “search” (Aronson and Sanderson 1987)); 10) eye flickering (= remaining motionless with rapid eye movements); 11) hovering with the tail curled; 12) hiding (= “hide” (Aronson and Sanderson 1987)); 13) opening mouth (= “yawn” (Aronson and Sanderson 1987)); 14) rubbing body on the surface (= “scratch” (Aronson and Sanderson 1987)); and 15) “bobbing” (= swimming forward while moving snout up and down), 16) “jumping” (= planktonic feeding), 17) cleaning, 18) being cleaned, and 19) other (that included: circling (*c.f* Reinboth (1973)), tailflick, and trying to instigate spawning).

Statistical analysis

To determine if group membership can be predicted from behavioural observations, I used discriminant function analysis (DFA) (Tabachnik and Fidell 1989, Morrison et al. 1992). Discriminant function analysis also reveals the degree of difference among groups with respect to the predictor variables (in this case, the behaviours). The DFAs were performed using the

DISCRIM model in SYSTAT 8.0 software.

Data from the 5-minute behavioural observations in 1997 were converted into percentages of occurrences, and then angular transformed to improve normality. All six behavioural categories were used as predictor variables: eating, swimming alone, swimming with others, aggression, hiding, and other behaviours. The grouping variables were life stages and species.

Data from the 10-minutes behavioural observations in 1998 and 1999 were also converted into percentages of occurrences, and then angular transformed to improve normality. I reduced the predictor variables to ten behaviours by eliminating the behaviours with lowest frequencies. The ten most common behaviours used in the DFA included (in order of decreasing frequency): swimming alone, eating, touching nose to the substrate, hovering, hiding, being chased by damselfish, looking at the substrate, "bobbing", eye flickering, and swimming with conspecifics. The dependent variables, or grouping variables, were life stages and species.

RESULTS

Behavioural study I: 5 -minute observations

From these general behavioural observations, I found that *Halichoeres bivittatus* and *H. maculipinna* had higher frequencies of eating than the other species (Figs. 3.1a - 3.1f). *Halichoeres maculipinna* and *Thalassoma bifasciatum* had lower frequencies of swimming alone than the other species, and higher frequencies of swimming with others. *Halichoeres garnoti* and *H. radiatus* had higher frequencies of hiding than the other species. Ontogenetically, juveniles and IP adults were very similar. The only qualitative differences were that *H. bivittatus* juveniles had lower frequencies of swimming alone than IP *H. bivittatus* (Fig. 3.1a), and *Thalassoma bifasciatum* IP adults had higher frequencies of swimming with other fishes than juvenile *T. bifasciatum*.

Although the life stages and species were significantly different (Wilk's Lambda = 0.403; $F = 3.914$, $df = 60, 1241$; $p = < 0.001$), there was a high degree of overlap among them. The DFA had a very poor ability to predict group membership. Only 20% of the 252 individuals observed were classified correctly, with a low of 0% for *T. bifasciatum* juveniles to a high of 54% for *H. radiatus* juveniles. The first discriminant function (DF1) explained only 55.6 percent of the total dispersion of observation points (Table 3.1). The canonical correlation for DF1 was also low and indicated that only 61% of the variance is shared between group membership (life stage and species) and the behaviours on each dimension. The behaviours that had the highest canonical discriminant scores for DF1 (Table 3.1, Fig. 3.2) were strong positive scores for swimming with others, and strong negative scores for hiding. The behaviours that had the highest canonical discriminant scores for DF2 were strong positive scores for eating and "other" behaviours.

There is a higher degree of overlap among IP adults of each species than juveniles (Fig. 3.2). *Halichoeres radiatus* and *H. garnoti* juveniles had fewer occurrences than the other species and life stages of swimming with others, eating, and swimming alone (their centroids are closest to the origin, Fig. 3.2). There are minimal ontogenetic shifts within a species, particularly *Halichoeres poeyi*, *H. bivittatus*, and *H. maculipinna* (there is high overlap between juvenile and IP ellipses). Biological interpretations from this analysis should be accepted with caution because of the poor ability to predict group membership. This may be due to 1) a high degree of overlap among these species and the life stages in reality, 2) the behaviours were extremely general and not sufficient enough to discriminate among the groups (they were typical labrid behaviours, and not distinctive behaviours of individual species), and 3) low sample sizes for some of the groups.

Behavioural study II: 4 sets of 10-minute observations

This study was a more detailed investigation of labrid behaviours. There were very few striking differences in the behavioural profiles between species (Figs. 3.3a - 3.3f). In general,

Halichoeres garnoti and *H. radiatus* had higher frequencies of hiding than the other species, *H. poeyi* had higher frequencies of eye flickering than the other species (which may be a behaviour that makes them more alert to threats), and *T. bifasciatum* had higher frequencies of swimming with conspecifics than the other species. There were some behaviours that shared a common ontogenetic trend among these species (Figs 3.3a - 3.3f). As labrids grow, they increase their frequencies of swimming alone, and decrease their frequencies of searching (= touching their nose to the substrate), and hovering with their tail curled. Hovering is assumed to put the individual in a better position to flee. Terminal phase individuals in each of the species tend to have lower frequencies of eating.

The groups were significantly different from each other (Wilk's $\lambda = 0.0019$; $F = 9.00$, $df = 180, 1722$; $p < 0.001$). There was a better ability in this study to predict group membership than in the first study. Sixty percent of the 207 individuals observed were classified correctly, with a low of 18% for *H. poeyi* IP adults, to a high of 80% for *H. bivittatus* IP adults. The first discriminant function (DFA) explained only 41.5 % of the total dispersion of observation points (Table 3.2). However, the canonical correlation for DF1 was very high and indicated that 91% of the variance is shared between group membership (life stage and species) and the behaviours on this dimension. The behaviours with the highest canonical discriminant scores for DF1 were strong negative scores for hiding, and strong positive scores for eating (Table 3.2, Fig. 3.4). The behaviours that had the highest canonical discriminant scores for DF2 were strong positive scores for swimming alone, and strong negative scores for eye flickering.

I had only small samples of terminal phase adults (ranging from 4 to 9 individuals). One recommendation for DFA is that the number of predictor variables used should not exceed the smallest sample size (Tabachnik and Fidell 1989). TP adults were thus removed from the data set, and another DFA was done on the remaining data. The groups were still significantly different

from one another (Wilk's Lambda: 0.0067; $F = 11.56$; $df = 100, 1143$, $p < 0.001$, Table 3.3).

Sixty-five percent of 178 individuals were correctly predicted; with a low of 10% for *H. radiatus* juveniles to a high of 88% for *H. bivittatus* IP adults. The number of correctly classified individuals was not consistently higher than those correctly classified in the analysis with TP adults included. Therefore, only the DFA plot for the entire data set is presented here (Fig. 3.4).

The first discriminant function separates the species (Fig. 3.4), and the second discriminant function separates life stages. Compared with other juveniles, *Halichoeres bivittatus* and *H. maculipinna* juveniles show the lowest frequency of hiding and the highest frequency of eating. Compared with the other life stages, *Halichoeres bivittatus* and *H. maculipinna* juveniles have higher frequencies of eye flickering and lower frequencies of swimming alone. *Halichoeres garnoti* and *H. radiatus* are easily discriminated from the other species and life stages because of the high frequency of hiding. An interesting component to this DFA, is that *Thalassoma bifasciatum*, although in a separate genus, is located in the center of the discriminant score plot (Fig. 3.4), with two species to the left of it, and 3 species to the right. This may be a result of restricting the behaviours in the analysis to the ten most common.

DISCUSSION

The most impressive observation during this study was the extremely low number of aggressive encounters among these ecologically and morphologically similar labrids. They are highly gregarious, and show extensive overlap in home range areas (*pers. obs.*), yet rarely act antagonistically towards one another. During the second behavioural study (1998 and 1999), I recorded 22,260 observations (= 123 hours and 40 minutes of observation time) of juvenile and initial phase adult labrids. Of these observations, 1,141 (or 5%) were chases by damselfish, 59 (or 0.3%) were chases by conspecific terminal phase adults, 57 (or 0.3%) were chases by conspecific

juveniles or adults, and 58 (or 0.3%) were chases by heterospecific juvenile or adult labrids, and only 17 (or 0.07%) were chases by predators (including trumpetfish (*Aulostomus maculatus*), yellowtail snapper (*Ocyurus chrysurus*), bar jack (*Caranx ruber*), coney (*Epinephelus fulvus*), and an algal frond moved with a current and caused a juvenile *H. poeyi* to quickly flee from its hovering position). Intra- and interspecific competition among these labrids are not important factors influencing their behavioural interactions. However, interactions with damselfish may be consequential to the spatial arrangements and movements of these labrids. I observed that during the summer months, labrids are active for 8 or 9 hours (480 to 540 minutes) each day; therefore, 5% of this time, or approximately half an hour each day is invested in agonistic encounters with damselfish.

Related labrid studies have found mixed results with respect to conspecific and heterospecific aggression (Tribble 1982, Jones 1984a, Fitch and Shapiro 1990). Tribble (1982) found low levels of aggression in another labrid, *Coris dorsomaculata*. Agonistic encounters between neighboring males only occurred 15 times during 35 hours of observation. Fitch and Shapiro (1990) found that only one in five encounters between *Thalassoma bifasciatum* individuals resulted in aggressive actions. However, Jones (1984a) found a great deal of aggression between similar-sized individuals of the temperate wrasse, *Pseudolabrus celidotus*.

The labrids I studied are highly social, and their social behaviour changes as they mature. Many of the behaviours were performed in the vicinity of conspecifics, heterospecific labrids, and juvenile parrotfishes and surgeonfishes (Jones, *unpublished data*). However, ontogenetically, these labrids increase the frequency of swimming alone as they grow. Schooling behaviour of fishes is acknowledged as a critically important anti-predator mechanism (Pulliam and Caraco 1984, Clark and Mangel 1986, Magurran 1990). The benefits of “many eyes” include easier detection of food and predators. More individuals in a school also lead to greater dilution and confusion of predators

which gives the school an advantage over solitary individuals when predators approach.. In this study, it was observed that social interactions decrease as labrids grow. Larger individuals invest more time swimming alone, possibly because they are more effective at escaping predation, or they are more efficient at finding food. There are trade-offs that could be explored using experimental manipulations.

Itzkowitz (1977b) examined the dynamics of mixed-species foraging groups composed of parrotfish, surgeonfish, butterflyfish, the goatfish *Pseudupeneus maculatus*, and the wrasse, *Halichoeres bivittatus*. He categorized wrasses as “opportunists” that frequently joined parrotfishes that were the “core” members of foraging assemblages. Solitary wrasses must devote a greater portion of time than schooling fish to scan for predators, which would reduce the time devoted to foraging. On the other hand, greater locomotion and exploratory behaviour in terminal phase individuals might allow them to explore a larger area per unit time and consequently give them a better chance to find a more profitable patch. In addition to an increase in the frequency of time spent swimming alone, I found that terminal phase individuals in each of the species tend to spend less time feeding and touching their noses to the substrate. This may be a result of finding more profitable patches due to greater mobility, but it could also be a result of ontogenetic changes in their jaw morphology which enables greater crushing strength. More profitable food items may not be available to smaller labrids because of jaw crushing limitations (Wainwright 1988). Indeed, Wainwright (1988) found that *Halichoeres garnoti*, *H. bivittatus*, and *H. maculipinna* exhibited considerable ontogenetic changes in diet as their jaw crushing ability reached a certain level.

The reduction in the frequency of searching behaviour as labrids grow may also be a result of ontogenetic changes in visual abilities. Although it has not been investigated in any of the species in this study, it is possible that juveniles do not have the same visual resolution as older members of their species, so rely more heavily on tactile searching (by touching their nose to the

substrate). Ontogenetic improvements in visual acuity and resolution have been found in other fish species. Wanzenboeck et al. (1996) found that behavioural measures of visual resolution improved with growth in the roach (*Rutilus rutilus*) and yellow perch (*Perca flavescens*). Ontogenetic improvements in reactive distances (as a result of changes in vision and mechanoreception) have also been demonstrated in Atlantic croaker larvae (Poling and Fuiman 1997). One final example to support my hypothesis is that age-0 yellow perch (*P. flavescens*) shift from pelagic to demersal waters when they reach standard lengths of 24-31 mm. This length corresponds to a higher level of visual acuity that enables a shift in diet to include a larger range of prey sizes and types (Wahl et al. 1993).

The biggest behavioural difference among species was in the frequency of hiding. All three life stages of *Halichoeres garnoti*, and juvenile *H. radiatus* have higher occurrences of hiding than the other species. There are two possible explanations for this: 1) qualitatively, I found these individuals to be more solitary than the other species (*pers. obs.*, and Thresher 1979); and 2) both *H. radiatus* and *H. garnoti* are more boldly coloured than the other species which makes them more conspicuous on the reef. To circumvent higher predation risk as a result of these two factors, they may spend more time out of sight from potential predators.

Individuals of different life stages but within the same species may be more different from one another than individuals of different species. Juvenile *Halichoeres bivittatus* and *H. maculipinna* showed greater behavioural overlap with each other than with initial phase conspecifics. This has been observed for other taxa by Wissinger (1992), who stated that “the ontogenetic size and/ or stage changes that occur in some taxa may be accompanied by shifts in diet and/or habitat to the extent that different individuals within the same population can differ in resource use by as much or more than that observed between different species”.

Concluding statements

The labrids in this study are ecologically and morphologically similar, and I have now demonstrated that they are ontogenetically similar with respect to behaviours. Despite the extent of these similarities, there was no evidence of competition among individuals. Instead, some of the results suggest labrids may benefit from joining foraging assemblages rather than remaining solitary (unless one has achieved the terminal phase status). These results may not be applicable to labrids in other locations, where resources or space may be limiting.

One potential research direction for this study is to investigate whether or not labrid behaviours are altered by the types of habitat available to an individual. Other authors have found evidence of habitat-mediated social behaviours (Brown 1971, Budaev 1997). Brown (1971) studied the mechanisms of competitive exclusion between two species of chipmunks, and found that the differences between the two species in aggressive behavior apparently represent adaptations to the density of cover and food resources in their habitats. Budaev (1997) found that labrids (*Symphodus ocellatus*) occupying vegetated habitats displayed much more pronounced schooling tendencies than those from open areas. It would be interesting to determine if ontogenetic shifts in behaviour of these six reef labrids are accompanied by ontogenetic shifts in microhabitat. In another labrid study, only two of the eight abundant species showed different patterns of habitat use by adults and recruits, suggesting ontogenetic shifts in habitat use (Green 1996). Chapter IV of my thesis looks at ontogenetic shifts in microhabitat use.

Table 3.1. Results of discriminant function analysis predicting species and life stage membership from six behavioural variables. Only the first three discriminant functions and their canonical correlations are shown, because the remaining three discriminant functions do not explain a large proportion of the total dispersion. Wilk's lambda = 0.403; F-statistic = 3.633 (df = 60, 1446); $p < 0.001$.

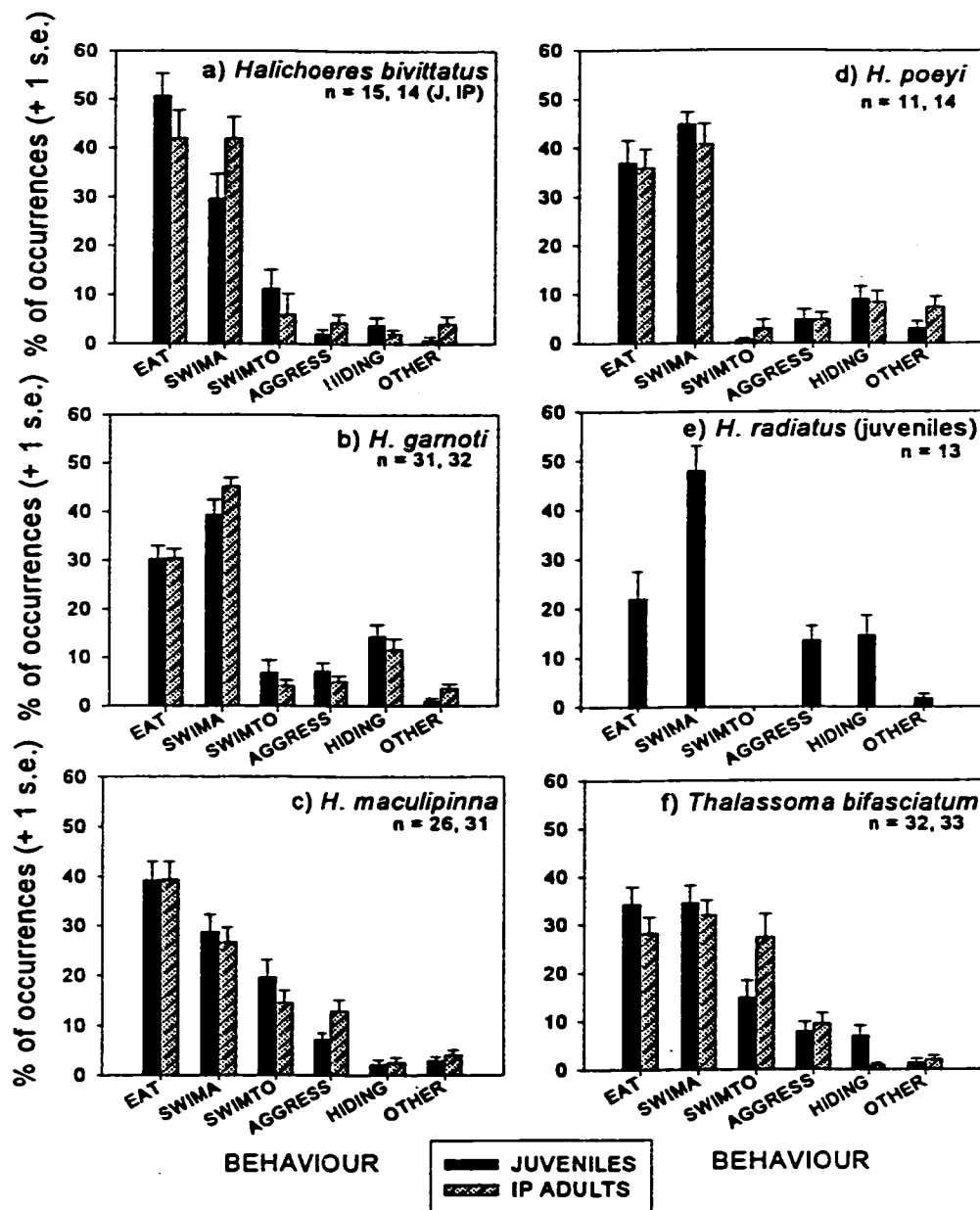
Discriminant Function:	DF1	DF2	DF3
Canonical Correlations:	61.0%	42.5%	32.0%
Cumulative Proportion of Total Dispersion:	0.556	0.763	0.870
BEHAVIOUR	canonical correlations:		
<i>eating</i>	0.194	0.538	0.365
<i>swimming alone</i>	-0.453	0.145	0.001
<i>swimming with others</i>	0.670	-0.431	0.129
<i>aggression</i>	0.105	-0.290	-0.836
<i>hiding</i>	-0.679	-0.007	0.047
<i>other</i>	0.050	0.522	-0.638

Table 3.2. Results of discriminant function analysis predicting species and life stage membership from ten behavioural variables. (Terminal phase adults are **included** in the grouping variables.) Only the first three discriminant functions and their canonical correlations are presented. Wilk's lambda = 0.0019; F- statistic = 9.00 (df = 180, 1722); $p < 0.001$.

Discriminant Function:	DF1	DF2	DF3
Canonical Correlation:	91.1%	86.7	78.6
Cumulative Proportion of Total Dispersion:	0.415	0.672	0.809
BEHAVIOUR:	canonical correlations:		
<i>swimming alone</i>	0.028	0.497	0.497
<i>eating/ biting at the substrate</i>	0.608	-0.368	0.556
<i>touching nose to the substrate</i>	0.331	-0.190	-0.168
<i>hovering with tail curled</i>	0.221	-0.101	-0.251
<i>hiding</i>	-0.736	-0.286	0.196
<i>chased by damselfish</i>	-0.126	-0.105	0.149
<i>look down at substrate</i>	-0.317	-0.373	0.047
<i>"bobbing"</i>	0.085	0.125	0.208
<i>eye flickering</i>	-0.156	-0.450	-0.368
<i>swimming with conspecifics</i>	0.208	0.263	-0.617

Table 3.3. Results of discriminant function analysis predicting species and life stage membership from ten behavioural variables. (Terminal phase adults are **excluded** from the grouping variables.) Only the first three discriminant functions and their canonical correlations are presented. Wilk's lambda = 0.0067; F- statistic = 11.56 (df = 100, 1143); $p < 0.001$.

Discriminant Function:	DF1	DF2	DF3
Canonical Correlation:	91.9	82.3	77.4
Cumulative Proportion of Total Dispersion:	0.517	0.718	0.861
BEHAVIOUR:	canonical correlations:		
<i>swimming alone</i>	0.136	0.092	0.461
<i>eating/ biting at the substrate</i>	0.687	-0.494	0.351
<i>touching nose to the substrate</i>	0.385	-0.154	-0.134
<i>hovering with tail curled</i>	0.344	-0.023	-0.450
<i>hiding</i>	-0.648	-0.184	0.185
<i>chased by damselfish</i>	-0.035	-0.266	0.053
<i>look down at substrate</i>	-0.235	-0.484	-0.120
<i>"bobbing"</i>	0.098	0.071	0.377
<i>eye flickering</i>	-0.088	-0.559	-0.686
<i>swimming with conspecifics</i>	0.358	0.526	-0.395



Figures 3.1 a - f. Results from the 5-minute behavioural observations (1997 data). Average frequency of occurrences of different behaviours (+ 1 s.e.). The solid bars represent juveniles, and the hatched bars represent initial phase adults. The sample sizes for each life stage and species are stated in each plot. EAT = eating, SWIMA = swimming alone, SWIMTO = swimming with others, AGGRESS = aggression, HIDING = hiding, OTHER = any additional behaviours.

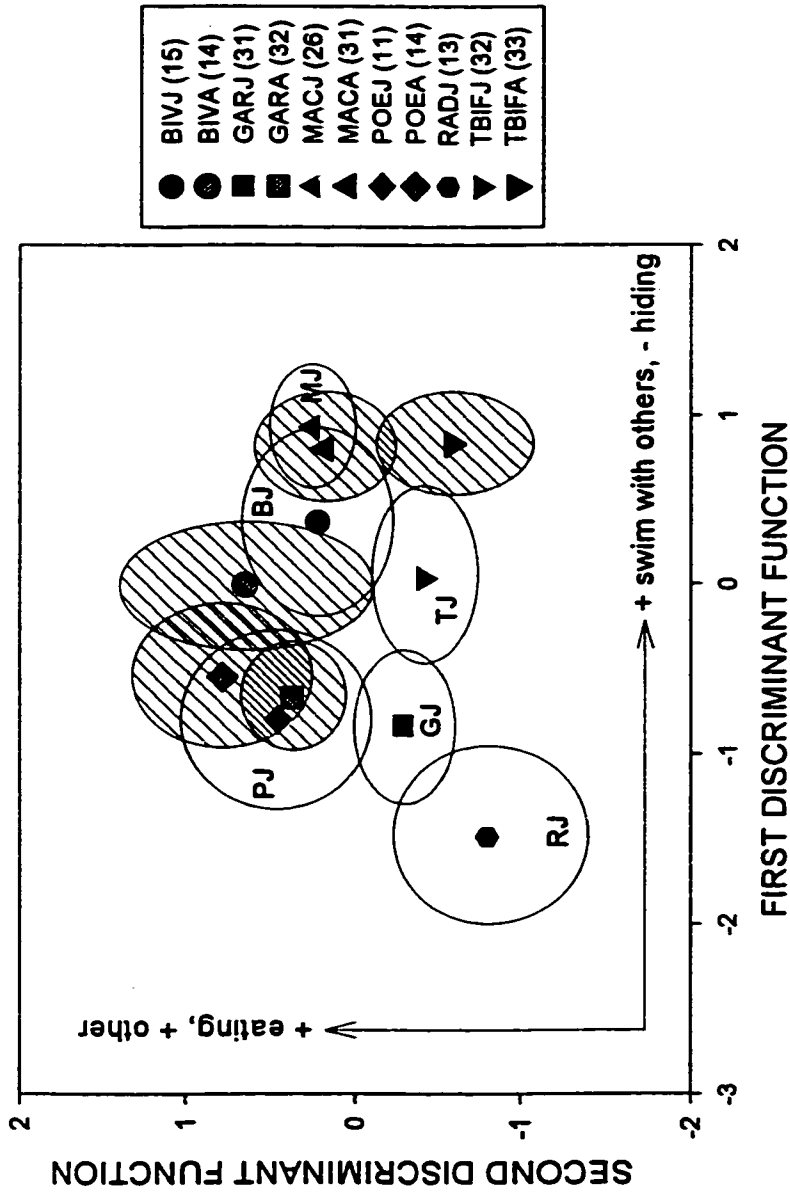


Figure 3.2. Discriminant Function plot of five-minute behavioural observations (1997). The centroids are plotted, and the ellipses encompass the 95% confidence intervals of the means. Open ellipses represent juveniles, and shaded ellipses represent initial phase adults. The sample size for each life stage and species is shown in the legend (the first three letters represent the species name: BIV = *Halichoeres bivittatus*, GAR = *H. garnoti*, MAC = *H. maculipinna*, POE = *H. poeyi*, RAD = *H. radiatus*, TBIF = *Thalassoma bifasciatum*; and the last letters represent the life stage: J = juvenile and IP = initial phase adults. Results of the DFA for these data are presented in Table 3.1.)

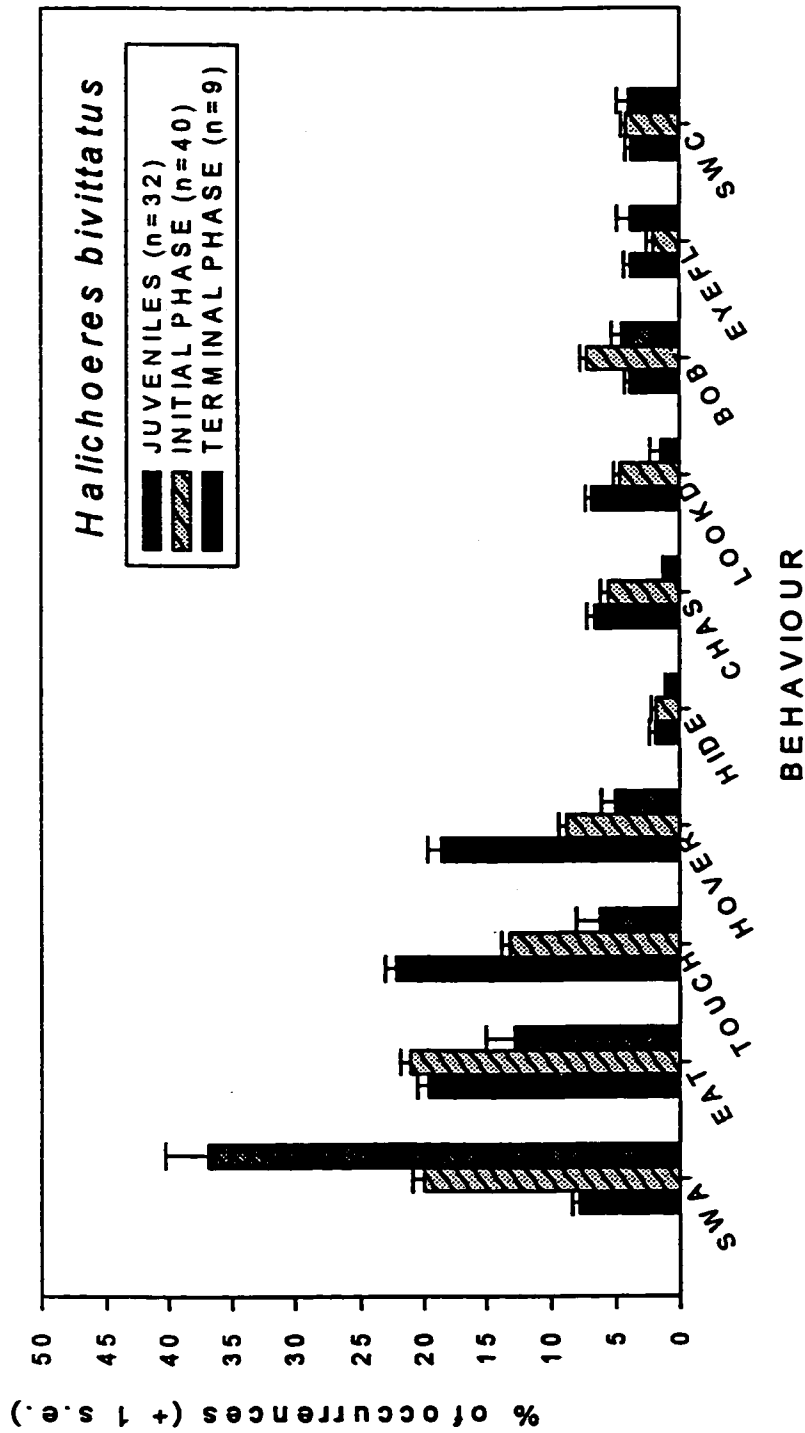


Figure 3.3 a. Results from the 10-minute repeated behavioural observations (1998 and 1999 data). Average frequency of occurrences of different behaviours (± 1 s.e.). The sample sizes for each life stage and species are stated in the figure legend. Behaviours are coded as the following: SWA = swimming alone, EAT = eating, TOUCH = touching nose to substrate, HOVER = hovering with tail curled, HIDE = hiding, CHAS = chased by damselfish, LOOKD = look down at substrate, BOB = bobbing up and down, EYEFL = eye flickering, SWC = swimming with conspecifics.

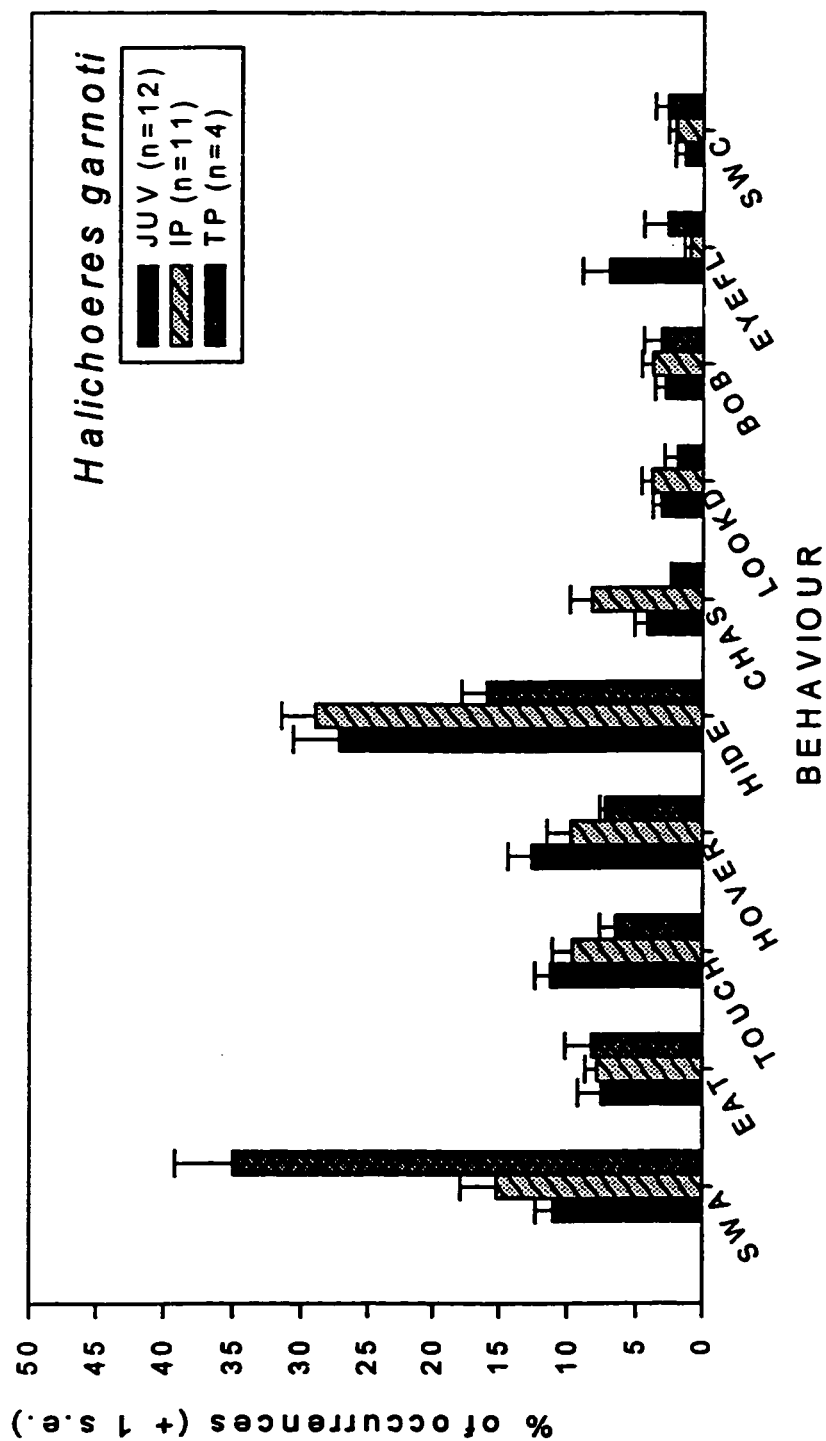


Figure 3.3 b. Results from the 10-minute repeated behavioural observations (1998 and 1999 data). Average frequency of occurrences of different behaviours (± 1 s.e.). The sample sizes for each life stage and species are stated in the figure legend. Behaviours are coded as the following: SWA = swimming alone, EAT = eating, TOUCH = touching nose to substrate, HOVER = hovering with tail curled, HIDE = hiding, CHAS = chased by damselfish, LOOKD = look down at substrate, BOB = bobbing up and down, EYEFL = eye flickering, SWC = swimming with conspecifics.

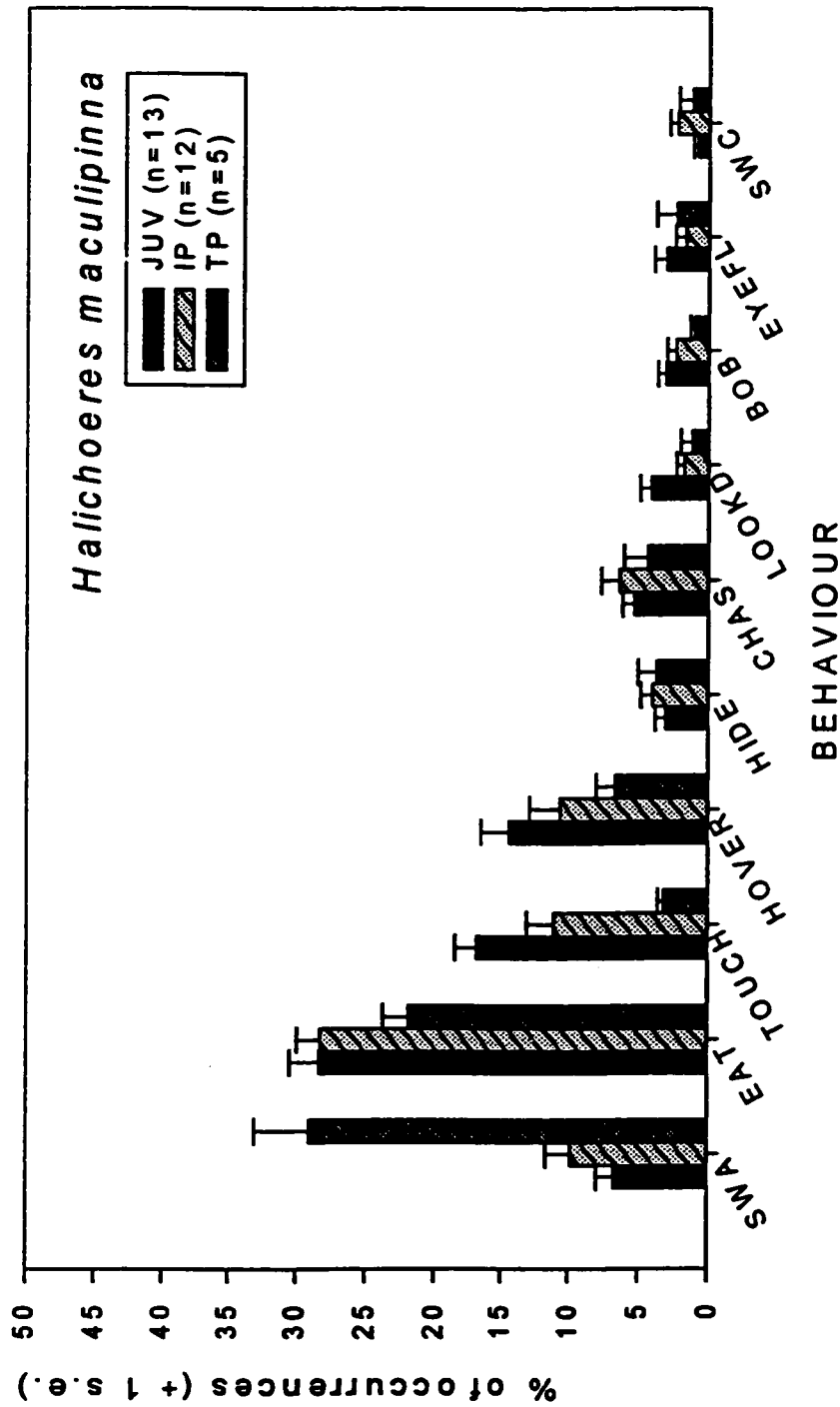


Figure 3.3 c. Results from the 10-minute repeated behavioural observations (1998 and 1999 data). Average frequency of occurrences of different behaviours (+ 1 s.e.). The sample sizes for each life stage and species are stated in the figure legend. Behaviours are coded as the following: SWA = swimming alone, EAT = eating, TOUCH = touching nose to substrate, HOVER = hovering with tail curled, HIDE = hiding, CHAS = chased by damselfish, LOOKD = look down at substrate, BOB = bobbing up and down, EYEF = eye flickering, SWC = swimming with conspecifics.

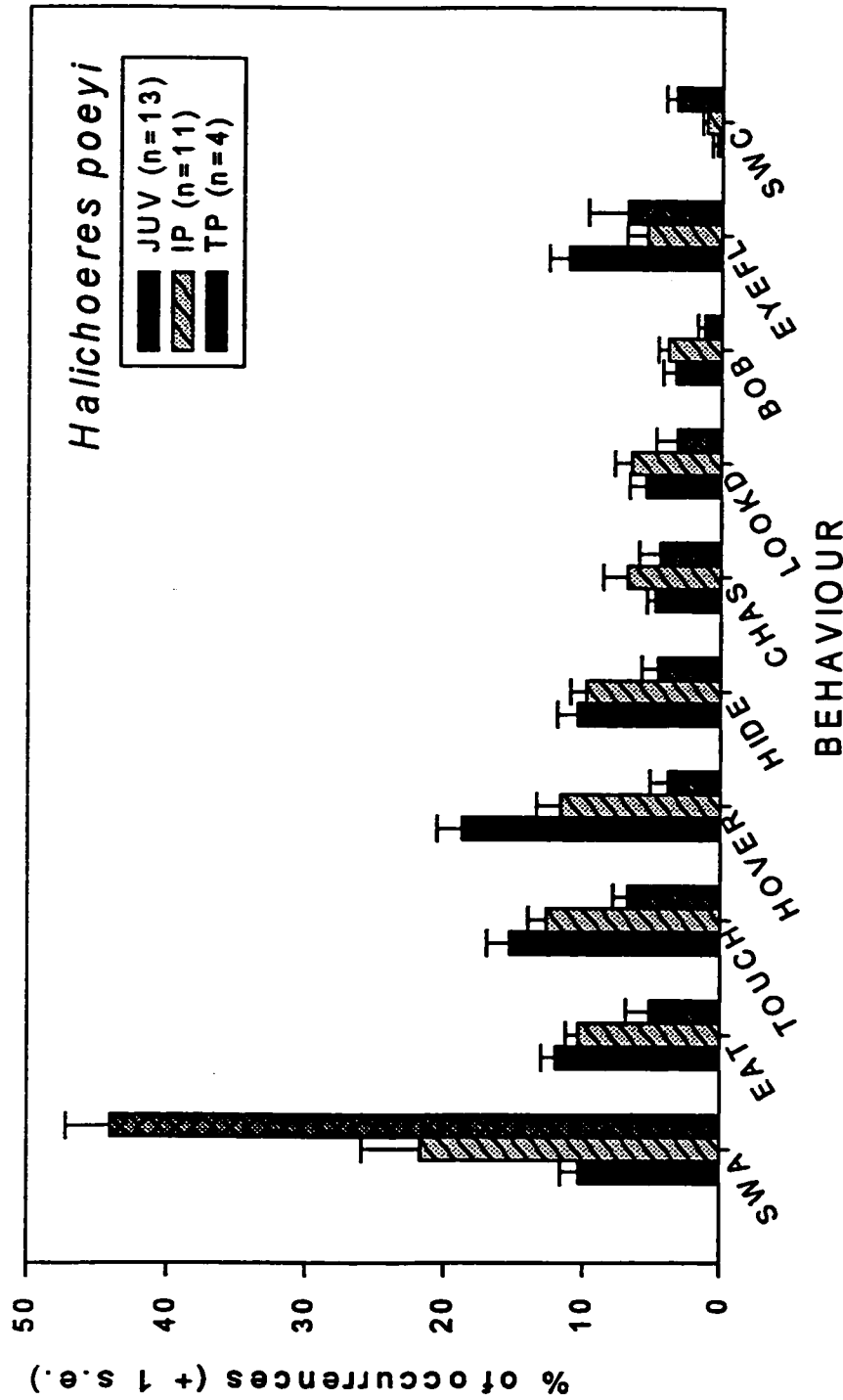


Figure 3.3 d. Results from the 10-minute repeated behavioural observations (1998 and 1999 data). Average frequency of occurrences of different behaviours (± 1 s.e.). The sample sizes for each life stage and species are stated in the figure legend. Behaviours are coded as the following: SWA = swimming alone, EAT = eating, TOUCH = touching nose to substrate, HOVER = hovering with tail curled, HIDE = hiding, CHAS = chased by damselfish, LOOKD = look down at substrate, BOB = bobbing up and down, EYFL = eye flickering, SWC = swimming with conspecifics.

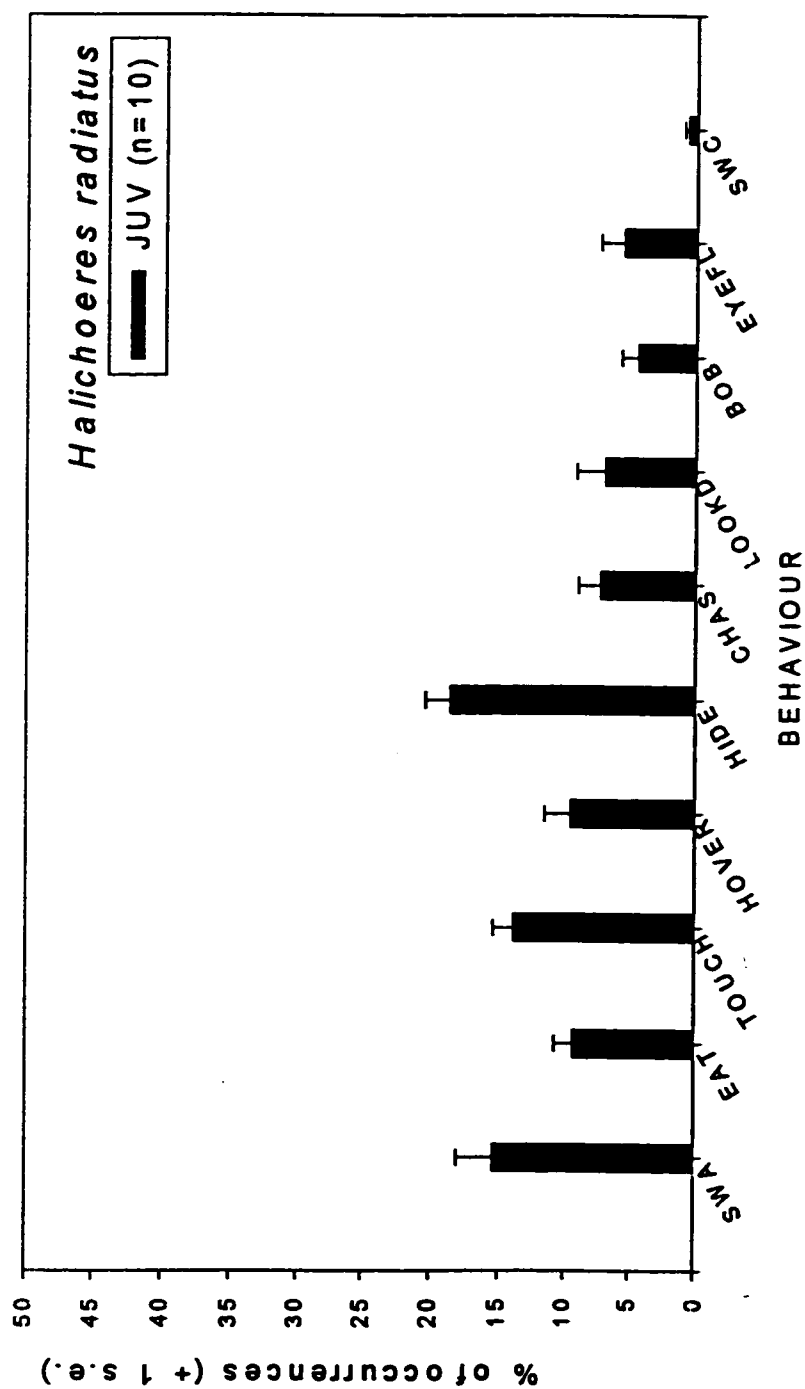


Figure 3.3 e. Results from the 10-minute repeated behavioural observations (1998 and 1999 data). Average frequency of occurrences of different behaviours (+ 1 s.e.). The sample sizes for each life stage and species are stated in the figure legend. Behaviours are coded as the following: SWA = swimming alone, EAT = eating, TOUCH = touching nose to substrate, HOVER = hovering with tail curled, HIDE = hiding, CHAS = chased by damselfish, LOOKD = look down at substrate, BOB = bobbing up and down, EYFL = eye flickering, SWC = swimming with conspecifics.

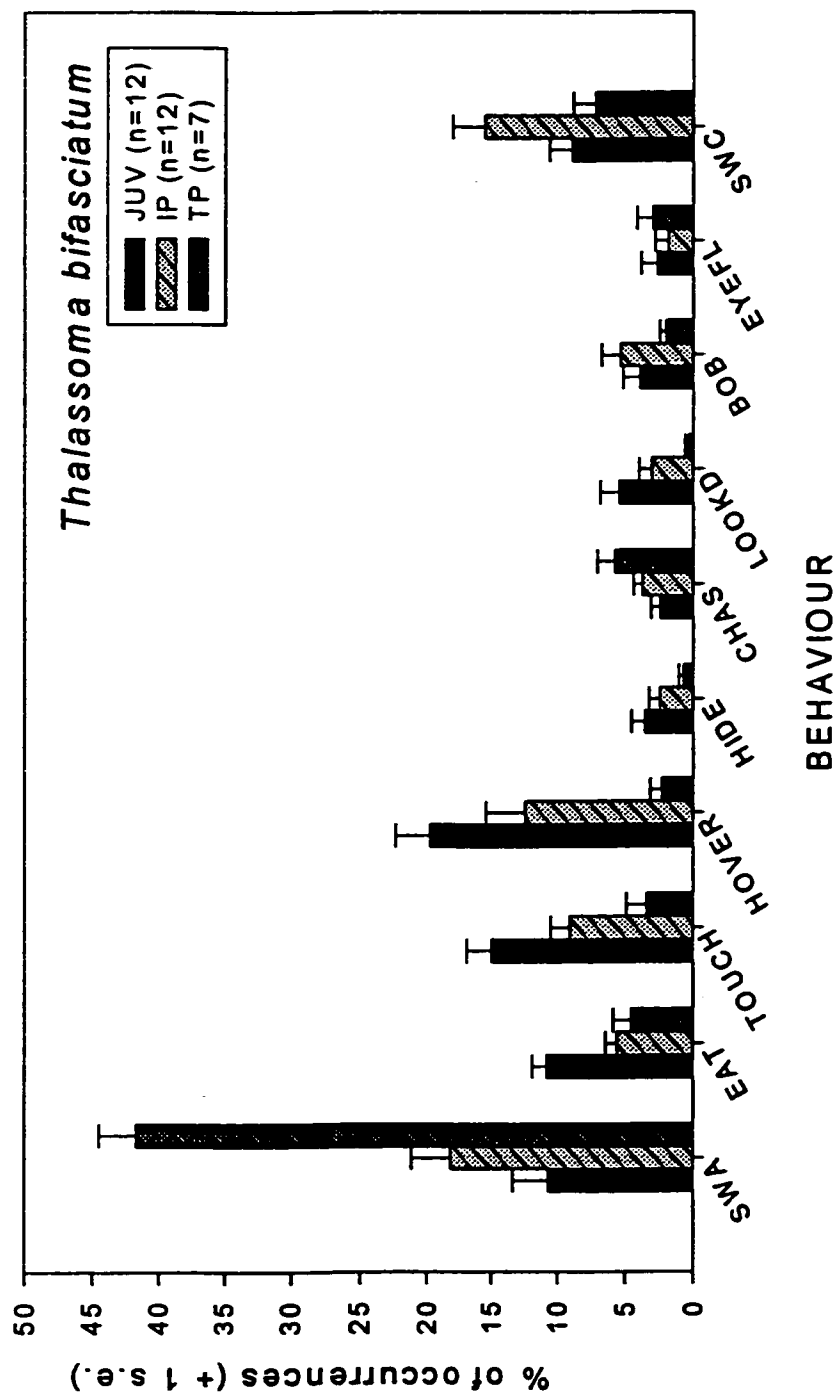


Figure 3.3 f. Results from the 10-minute repeated behavioural observations (1998 and 1999 data). Average frequency of occurrences of different behaviours (± 1 s.e.). The sample sizes for each life stage and species are stated in the figure legend. Behaviours are coded as the following: SWA = swimming alone, EAT = eating, TOUCH = touching nose to substrate, HOVER = hovering with tail curled, HIDE = hiding, CHAS = chased by damselfish, LOOKD = look down at substrate, BOB = bobbing up and down, EYEFL = eye flickering, SWC = swimming with conspecifics.

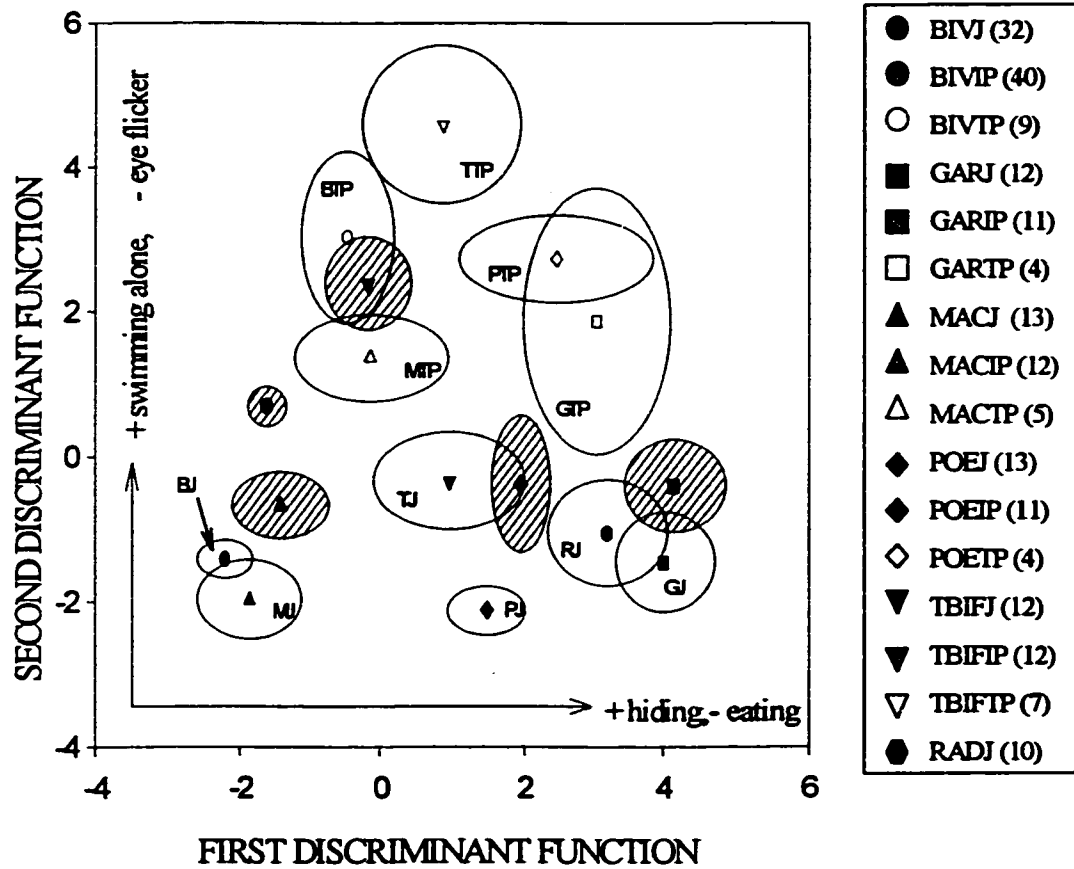


Figure 3.4. Discriminant Function plot of 1998 and 1999 data comprised of a minimum of 4x10 minute repeated observations of the same individuals. The centroids are plotted, and the ellipses encompass the 95% confidence intervals of the means. The sample size for each life stage and species is shown in the legend (the first three letters represent the species name: BIV = *Halichoeres bivittatus*, GAR = *H. garnoti*, MAC = *H. maculipinna*, POE = *H. poeyi*, RAD = *H. radiatus*, TBIF = *Thalassoma bifasciatum*; and the last letters represent the life stage: J = juvenile, IP = initial phase adults, and TP = terminal phase adults. Results of the DFA for these data are presented in Table 3.1. Legend shows the sample sizes for each life stage and species (n). Results of the DFA for these data are presented in Table 3.2.

CHAPTER IV

THE DISTRIBUTION OF BEHAVIOURS AND SPECIES INTERACTIONS WITHIN HOME RANGE ISOPLETHS IN FIVE CARIBBEAN WRASSE SPECIES (FAMILY LABRIDAE)

ABSTRACT

Many demersal fishes possess home range areas which are typically irregular in shape. These irregularities may be explained by haphazard movements of the fish, selective microhabitat use, or behavioural interactions with neighbouring fishes. This study investigated the distribution of behaviours and species interactions throughout home range isopleths in five Caribbean labrid species: *Halichoeres bivittatus*, *H. garnoti*, *H. maculipinna*, *H. poeyi*, and *Thalassoma bifasciatum*. Isopleths encompass an area containing a user-defined percentage of observation points of the focal fish. In this study, the 30% isopleth defined the core use area, the 30-75% isopleths defined the intermediate activity area, and the 75-95% isopleths defined the peripheral region of the home range. In general, I found that some behaviours were randomly distributed throughout home range isopleths whereas other behaviours were non-randomly distributed. *Halichoeres bivittatus* showed a higher frequency than expected eating in their core use areas, and 59% of the individuals observed showed a higher frequency than expected being chased by damselfish in the peripheral region of their home ranges. *Halichoeres garnoti* showed a higher frequency than expected eating + touching nose to the substrate and a lower frequency than expected swimming with other individuals in their core use areas, and 64% of the individuals

observed showed a higher frequency than expected being chased by damselfish in the peripheral region of their home range areas. In general, *H. maculipinna* exhibited a random distribution of behaviours throughout their home ranges, with a non-significant trend for more agonistic interactions with damselfish in peripheral regions of their home ranges. Both *H. poeyi* and *Thalassoma bifasciatum* showed higher frequencies than expected being chased by damselfish in the periphery of their home ranges. *Thalassoma bifasciatum* showed a higher frequency than expected eating + touching nose to the substrate in their core use areas. Overall, the non-random distribution of agonistic interactions with damselfish throughout home ranges suggests a large influence of the position of damselfish on the spatial arrangements of these labrid species.

INTRODUCTION

Spatial dynamics (i.e. space use and movement) are often regarded as the most fundamental demographic processes that influence ecological patterns of populations and communities (Barrett 1995, Zeller 1997). Many demersal fishes possess home ranges or territories, and the degree of site fidelity and territoriality may have profound effects on the spatial arrangement of other species occupying the same area. For sedentary species, there are many factors that can affect home range characteristics: 1) size of animal (Schoener 1968, Simon 1975, Cole 1984, Barrett 1995, Kramer and Chapman 1999, Overholtzer and Motta 1999), 2) habitat geometry (Stamps et al. 1987, Eason and Stamps 1992), 3) composition of neighbours (Davies and Houston 1984, Norman and Jones 1984, Stamps et al. 1987, Wauters and Gurnell 1999), 4) resource availability and distribution (McNab 1963, Davies and Houston 1984, Alberts 1993, Hews 1993, Gerking 1994, Eifler 1996, Rolando 1998), and 5) distribution of mates (Deslippe and M'Closkey 1991, Hews 1993).

Many advances have been made in the field of terrestrial ecology with respect to

monitoring habitat use and home range dynamics in mammal populations (Dixon and Chapman 1980, Worton 1989, Gallerani Lawson and Rodgers 1997), lizard populations (Stamps and Eason 1989, Eifler 1996), and other taxa (e.g. birds (Rolando 1998)). Several of these techniques have been employed in fish ecology to study fish movements and habitat use, including radiotelemetry (e.g. Holland et al. 1993, Chilton and Poarch 1997, Szedlmayer 1997, Zeller 1997, Parkinson et al. 1999) and mark-recapture programs (Goforth and Foltz 1998). These types of studies are useful for large or highly mobile fishes but give very limited data on the activities, microhabitat use, or social interactions of the focal individuals. Aquatic researchers have also employed direct visual observations of fishes in their natural habitats because the aquatic environment often provides excellent surveillance conditions. Direct visual observations have been conducted with marking or tagging (e.g. fin clipping (Sale 1971), subcutaneous dyes (Thresher 1979), tags (Nursall 1977)), and without tagging (Reese 1973, Nursall 1974, Freeman and Alevizon 1983). There are drawbacks of direct visual observation because the close physical presence of a diving observer disturbs the fishes, and the time periods of observation are typically very small. I attempted to minimize these disadvantages in this study by using repeated visitations of focal fishes over a longer time frame relative to other studies.

Home range boundaries of fishes are commonly irregular and are often thought to be oriented with irregularities on the bottom, such as rock or coral structures (Nursall 1974, Reese 1978, Gerking 1994). Within the home range, activity is often concentrated into single or multiple activity centers containing important resources such as nests, refuges, or food sources (Warden and Lorio 1975, Nursall 1977, Gerking 1994, Bradbury et al. 1995, Coleman and Wilson 1996, Chilton and Poarch 1997, Zeller 1997). Single activity centers have been observed in many fish species. Nursall (1977) quantified the amount of time the redlip blenny, *Ophioblennius atlanticus* (Blennidae), spends in different parts of its territory. This fish spends about 99% of its time within

about 50% of its territory and about 80% of its time within about 5% of its territory. Another example of single activity centers within home range areas occurs in the temperate marine labrid, the cunner, *Tautoglabrus adspersus* (Bradbury et al. 1995). Females of this species spend 60% of the time in 24-32% of their home range area. Similarly, Chilton and Poarch (1997) found that a freshwater fish species, the grass carp, *Ctenopharyngodon idella* (Cyprinidae) uses only 16% of its total home range area for its 50% core use area. Multiple activity centers have also been found in several fish species as evidenced by disproportionate amounts of time being spent in more than one localized area within larger areas of movement (e.g. the largemouth bass, *Micropterus salmoides* (Centrarchidae) (Warden and Lorio 1975), and the coral trout, *Plectropomus leopardus* (Serranidae) (Zeller 1997)).

Few studies on home range use in fish have examined either the reasons for irregularly-shaped boundaries, or quantified the distribution of activities throughout home range areas. Zeller (1997) investigated microhabitat availability in the activity centers of *Plectropomus leopardus*, but did not analyse behaviours or social interactions at these locations. Nursall (1977) determined that the activity centers for *Ophioblennius atlanticus* were lookout posts, or resting spots where the fish sits for long periods and from which it is able to survey most of its territory. In a similar study, Cole (1984) observed activity centers within home ranges of the temperate marine goby, *Coryphopterus nicholsi* (Gobiidae). Their areas of activity were characterized primarily by feeding and station maintenance (i.e. sitting on the substrate, under cover, or perching on a rock). Aggressive events occurred mainly on the periphery of areas of activity, while feeding occurred both peripherally and centrally, and station maintenance was predominantly central to areas of activity. Coleman and Wilson (1996) investigated aggression, predator avoidance, and feeding rate in juvenile pumpkinseed sunfish, *Lepomis gibbosus* (Centrarchidae) as a function of location within their home range. They found that juvenile sunfish had a higher feeding rate in the center of

their home range than on the periphery. They found that aggression and predator avoidance did not appear to be important determinants of home range size in their study. Recently, Matsumoto et al. (1999) found that aggression between two temperate labrids, *Pseudolabrus eoethinus* and *P. sieboldi*, usually occurred near the border of the participants' home ranges. They suggested that this was one of the factors restricting home range size of these wrasses. Aside from these studies, we know little about the distribution of behaviours throughout home ranges. Although fishes exhibit disproportionate space use, are behaviours also non-randomly distributed throughout home range areas? If so, might they contribute to the irregularities in home range shape and positioning? This study investigates the distribution of behaviours and social interactions throughout the home ranges of several coral reef fish species (family Labridae).

There are various behaviours that characterize the Caribbean labrids used in this study. Four of the species belong to the *Halichoeres* genus (*H. bivittatus*, *H. garnoti*, *H. maculipinna*, *H. poeyi*) and are commonly seen foraging with conspecifics and heterospecifics, including juvenile members of the parrotfish (Scaridae) and surgeonfish (Acanthuridae) families (Roede 1972). Minimal agonistic encounters occur among members of foraging groups. The other species used in this study is *Thalassoma bifasciatum*, and although it is also highly social with heterospecifics, it is more commonly seen interacting with conspecifics. These foraging associations are likely to influence the spatial dynamics of these labrid species. Interspecific feeding associations have been reported for a variety of vertebrates (Morse 1977, Bertram 1978, Krebs and Davies 1987), most often for tropical and temperate reef fishes (Ehrlich and Ehrlich 1973, Fishelson 1977, Morse 1977, Ormond 1980, Aronson and Sanderson 1987, Baird 1993, Matsumoto et al. 1999).

All of the *Halichoeres* species in this study are known to feed on a variety of food items within the reef and are highly opportunistic (Roede 1972). *Thalassoma bifasciatum* feeds planktonically as well as demersally, and is also opportunistic (Randall 1967). Labrids are also

known egg predators of territorial damselfish (Pomacentridae), and damselfish aggressively defend small territories to protect food resources and their eggs. It has been shown that damselfish are capable of species-specific recognition, and alter their levels of aggression according to the invading species (Katzir 1981, Thresher 1976). Studies have shown lower levels of aggression by damselfish towards conspecifics and carnivorous fishes than towards labrids (Keenleyside 1972, Ferreira et al. 1998). Agonistic interactions with damselfish may therefore also be determinants of labrid home range shape and the distribution of behaviours throughout home range areas.

The main purpose of this study is to integrate an examination of space use with observations on behaviour and social interactions. This can be separated into specific questions: 1) Do these labrids feed or swim alone more frequently in the core use areas of their home ranges compared to peripheral regions? 2) Do the core use areas provide refuges from agonistic encounters with damselfish? 3) Do labrids swim with other fishes more often in the center or in the peripheral part of their home range?

METHODS

Study site

All home range maps and behavioural observations were recorded while snorkeling on contiguous stretches of the back reef of Tague Bay, St. Croix, U.S.V.I. (17°36'N, 64°36'W). Most fish observations were carried out at a depth less than 3 m. Algae growing on coral rubble (algal turf) was the predominant substratum, followed by dead *Porites porites*, dead *Acropora palmata*, other small, broken pieces of dead coral, and sand. Other live corals such as *Siderastrea* spp., *Diploria* spp., and *Agaricia* spp., as well as gorgonians, sponges, and seagrass beds (mostly *Thalassia testudinum*) occurred but were less common. These studies were carried out from May-August in 1998 and 1999. In this area, similar to many shallow reefs throughout the Caribbean, many coral heads and patches of algal turf are actively defended by small, territorial damselfishes.

The damselfish that was most common in the study area was the beaugregory damselfish, *Stegastes leucostictus*.

Study animals

Initial phase adults (i.e. sexually mature but not yet terminal phase) of the following labrid species were studied: *Halichoeres bivittatus*, *H. garnoti*, *H. maculipinna*, *H. poeyi*, and *Thalassoma bifasciatum*. It is fairly easy to recognize the different species based on colour differences, and among individuals within a species by colour, size, and distinctive markings. All the labrids in this study are protogynous hermaphrodites (Warner et al. 1975, Warner and Robertson 1978). They occur in at least two colour phases, and three sexual types. Males are born as males (primary males), or have originated from females that have changed sex to become males (secondary males). Terminal phase males typically originate from the larger primary or secondary males that change colour, morphology, and behaviour to take over this role in a population. Only initial phase individuals were included in this study. General ecological, taxonomic, and behavioural information on these species is provided in Randall (1967), Bohlke and Chaplin (1968), Roede (1972), and Warner and Robertson (1978).

In 1998, individual fishes of all species were caught with a lift net (see Roede 1972) and tagged with beaded Floy® tags to verify the sedentary nature of these labrids. The fishes were anaesthetized with clove oil prior to tagging (Munday and Wilson 1997). The fishes quickly regained consciousness and resumed normal behaviours. Tagging therefore did not appear to greatly influence the behaviour of labrids. After these preliminary investigations, I found that individual labrids could be reliably identified without catching and tagging by recognizing differences in facial markings, lateral line deformities, and/or size differences.

Home range mapping

In order to map home ranges, quadrats (10x10 m²) were randomly marked on the reef with flagging tape. The habitat features of each quadrat were mapped on a slate. Mylar film was then placed over the map to record the positions of an individual fish during each observation period. Observation periods occurred between 0800 hr and 1500 hr, during this time labrids were constantly active. Observation periods were aborted if the focal individual was involved in a spawning period (which often occurs outside of the normal home range area). Observations were also not carried out on days when visibility fell below 10m (during storm events or algal blooms), because the fish were behaving abnormally. Individual fishes were randomly selected from each quadrat for observation. Each observation period lasted for 10 minutes, and at every 20 second interval, the position and several aspects of the behaviour of the focal fish were recorded (for a total of 30 points per observation period). To improve my estimates of home range area and behaviours, I used repeated observations on focal individuals. The time of day an individual was observed was randomized. A minimum of four observation periods were recorded for each focal individual in this study, resulting in a minimum of 120 observation points per focal individual (spread out over a period of approximately two weeks per individual). In a preliminary study, I found that a fifth set of observations did not substantially change the calculations of home range areas and activity centers (Mann Whitney T = 986.00; p = 0.812). Thus only four sets of observations were conducted on subsequent focal individuals.

Home range calculations and evidence of activity centers

The recorded positions were transferred into Cartesian coordinates and then analysed in the program CALHOME (Kie et al. 1994) to calculate the home range area and core use areas through the adaptive kernel (AK) method (Worton 1989). Examples using this method of calculating point percentage contours (30%, 75%, and 95%) for home range areas are given in Figure 4.1. For

adaptive kernel estimates, the smoothing parameter (which creates point percentage contours, or isopleths) was not preset. Instead, by default, the program estimates an optimal smoothing parameter by minimizing the least squares cross-validation scores which is a measure of how well the smoothing parameter fits the data (Worton 1989, Kie et al. 1994). The smoothing parameter is affected by the distribution or clustering of the observation points. The resultant isopleths delineate areas of probable visitation that may extend beyond the areas of actual visitation (Worton 1989). Although most studies involving animal movement use the Minimum Convex Polygon method to calculate home range area, those results will not be presented in this study (but see Chapter II) because it assumes that home range shape is convex, and it was not designed to examine centers of activity of core areas within home ranges (Anderson 1982, Gallerani Lawson and Rodgers 1997).

Because animals occasionally make exploratory excursions outside their areas of normal activity, the home range is commonly specified as an area within which some fixed percent of activity falls (most often 95%)(Anderson 1982; Worton 1989). This study employs calculations of the 30%, 75% and 95% isopleths (see Fig. 4.1). In this study, the 30% isopleth delineates the core use area to define a very tight cluster of observation points for the activity center. The area between the 30 and 75% isopleths delineates the middle area of the home range, and the area between the 75 and 95% isopleths delineates the peripheral region of the home range. These percentages are based on the distribution of observation points; they need not correspond to percentages of home range area. Depending on the concentration of points, CALHOME sometimes delimited more than one activity center. In those cases, the separate areas were combined to provide the total area covered by the 30% isopleth.

If observation points are randomly spread throughout the home range area, then percentage of area covered by the isopleth would be equivalent to the value of that isopleth (e.g. 30% AK =

30% of home range area). If points are clustered into activity centers, then the percentage of area covered by the isopleth would be less than the value of that isopleth. To investigate this, the ratio of AK 30% (in m²) : AK 95% (in m²) was calculated. This value should be equivalent to 31.6% of the home range area (= 30/95) if points are randomly distributed throughout the home range area.

Distribution of behaviours and social interactions within individual home ranges

While recording the movements of focal individuals on maps, I simultaneously recorded their behaviours on the same 20 second schedule. The behaviours used in this study consisted of the following ecologically important behaviours (other behaviours were recorded but were analysed for a different purpose in Chapter III): EAT = eating/biting, EATTOUCH = eating + touching substrate with nose, CHASED = being chased by damselfish (aggressive acts by damselfish are characterized by chasing and biting and labrids typically swim in the opposite direction (Shulman 1985, Itzkowitz 1990, Fitch and Shapiro 1990), SWIMALO = swimming alone; SWIMOTH = swimming with conspecifics and heterospecifics, ACTOTH = swimming with others + all behaviours that were performed with at least one fish within two body lengths of the focal individual, or apparently performing the same behaviours in synchrony with the focal individual (as per Breder 1959). The frequency of occurrences of these behaviours was analysed among the species. In order to determine the distribution of behaviours throughout home ranges, isopleths calculated in CALHOME were overlayed onto an x,y coordinate graph in SigmaPlot with each of the activities labeled with letters (for examples, see Fig. 4.2 and 4.3). Each of the activities were then tallied within the isopleths, and compared to the total number of times that activity was performed (out of 120) for the focal individual. If behaviours are randomly distributed throughout the home range, then 31.6% of the observation points for each activity should be found within the 30% isopleth; 47.4% between the 30 and 75% isopleth, and 21% between the 75 and 95% isopleths (after compensating for elimination of 5% of the observation points).

Statistical analysis

To determine if there were differences among the species with respect to behaviours, the percentage of occurrences of activities was examined using one-way ANOVA for each activity, with species as the main effect. Data were angular transformed prior to analysis. This transformation normalized the data and homogenized the variances. Where a significant difference among species in transformed data was found, Tukey's *post hoc* tests of multiple comparisons were conducted to determine which species differed from the others. These analyses were performed in SYSTAT with an unbalanced GLM design (due to uneven sample sizes).

To determine if the activities are non-randomly distributed throughout home ranges, χ^2 goodness-of-fit tests were performed for each activity separately (see Zar 1996 for methods). Species were also analysed separately. If behaviours are randomly distributed throughout the home range, then they should conform to a 30:45:20 ratio based on the isopleths used in this study. Data were not transformed prior to analysis because χ^2 goodness-of-fit tests are performed on raw integer data.

RESULTS

Home range characteristics and evidence of activity centers

During this study I recorded 399 activity periods on 94 focal individuals distributed over the five species. Data for each species are based on a minimum of 4 activity periods over 11 focal individuals. Total lengths for the individuals used in this study ranged from an average of 7.4 cm for *Thalassoma bifasciatum* to 11.9 cm for *H. maculipinna* (Table 4.1). Individuals of each species were randomly chosen for inclusion in this study. *Thalassoma bifasciatum* on Tague Bay are typically smaller than the other species and reach a maximum size of approximately 13 cm TL, whereas the other species sometimes exceed 15 cm TL (e.g terminal phase *H. bivittatus* and *H.*

garnoti). Activity centers ranged from 2.4 to 4.0 m² in these labrids (Table 4.1). Area covered by the 75% isopleth ranged from 11.3 to 19.2 m². Home range area (95 % Adaptive Kernel) ranged from 26.5 to 48.8 m². *Halichoeres maculipinna* tends to have larger home ranges than the other species. Additionally, *Thalassoma bifasciatum* also tends to have larger home range areas relative to body size. The 30% AK isopleth contains 30% of the observation points, but only covers 8 to 16 % of the home range area. The smaller the area, the more tightly clustered the observation points are in the activity center relative to the overall home range area. (A more extensive analysis of home range parameters for these labrids can be found in Chapter II).

Frequencies of behaviours

There were several differences among the species with respect to the frequency of occurrences of different activities (Fig. 4.4). All species showed higher frequencies of eating + touching nose to the substrate than being chased by damselfish, swimming alone or swimming with others. Furthermore, 20 to 45% of their behaviours are performed while interacting with other fishes (ACTOTH). *Halichoeres bivittatus* and *H. maculipinna* showed significantly higher frequencies than the other species eating/ biting at the substrate (EAT), and eating + touching nose to the substrate (EATTOUCH). *Halichoeres bivittatus* showed significantly lower frequencies of agonistic encounters with damselfish than *H. garnoti* and *H. maculipinna*. *Halichoeres bivittatus* also showed a significantly higher frequency of swimming alone than all other species except *H. poeyi*. *Thalassoma bifasciatum* showed a significantly greater frequency of swimming with others than all the other species except *H. maculipinna*. *Halichoeres maculipinna* showed a significantly higher frequencies of activities with other fishes than the other species. *Halichoeres bivittatus* displayed a high degree of variability among individuals with respect to this activity (note the large standard error bar, Fig. 4.4). Overall, there were intermediate differences among species in behavioural frequencies.

Distribution of behaviours within home range areas

Despite the significant differences among species with respect to behavioural frequencies, there were some similarities among the species in the distribution of these activities throughout their home ranges. Most species appeared to spend more time being chased by damselfish in the peripheral regions of their home range areas, and with a few exceptions, most of the other activities were randomly distributed throughout the entire home range area (Figs. 4.5 - 4.9).

Table 4.2 details the results of statistical analyses. Many behaviours were randomly distributed across home ranges, but a few were not, and in some cases focal individuals within a species displayed heterogeneous results. Feeding behaviour was non-randomly distributed in several species. *Halichoeres bivittatus* spent a greater amount of time eating in their core activity area than throughout the rest of their home range (EAT, Fig 4.5). *Halichoeres garnoti* and *Thalassoma bifasciatum* spent more time eating + touching nose to the substrate in the core use areas of their home range than expected (EATTOUCH, Figs. 4.6 and 4.9). *Halichoeres maculipinna* and *H. poeyi* displayed a random distribution of eating and touching nose to the substrate throughout their home ranges (Figs. 4.7 and 4.8).

Aggression by damselfishes was the other behaviour most frequently non-randomly distributed. Most of the encounters with damselfish occurred in the peripheral area of their home ranges. However, for this behaviour, there were often heterogeneous responses within species, perhaps depending on the variation or availability of damselfishes at individual home ranges. *Halichoeres bivittatus*, *H. garnoti*, and *H. maculipinna* were not homogeneous with respect to the distribution of agonistic interactions with damselfish throughout their home ranges (Table 4.2). Separate χ^2 tests on the distribution of chases by damselfish revealed that 26 out of 44 *H. bivittatus*, 7 out of 11 *H. garnoti*, and 4 out of 13 *H. maculipinna* did not conform to the expected ratio of 30:45:20. For these individuals, more agonistic encounters than expected occurred in the

peripheral isopleth (Fig. 4.5, 4.6, and 4.7). Homogeneous samples of behavioural distributions were obtained for *H. poeyi* and *T. bifasciatum*, and both species showed more agonistic interactions than expected in the periphery of their home ranges (Figs. 4.8, and 4.9).

One final significant result was that *H. garnoti* spent more time than expected swimming with other individuals in the middle regions of their home ranges (between the 30 and 75% isopleths) (Fig. 4.6).

DISCUSSION

This study has shown that these Caribbean labrids (*Halichoeres bivittatus*, *H. garnoti*, *H. maculipinna*, *H. poeyi*, and *Thalassoma bifasciatum*) use activity centers differentially within their home ranges. Thirty percent of their time was spent in a core use area of only 8 to 16 % of their home range area. Additionally, there were differences in the frequency of occurrences of certain behaviours for each species. Despite these differences, there were similarities among these species with respect to the distribution of activities throughout home range areas. Some behaviours were randomly distributed throughout home ranges, and others were non-randomly distributed. There were several ecologically important behaviours that I hypothesized would occur more often than expected in the activity centers, including: eating, eating + touching nose to the substrate, and swimming alone. I also hypothesized that fewer agonistic encounters with damselfish would occur in the activity centers than expected from random distributions of behaviours. These hypotheses are based on the assumption that the central area within the home range provides a refuge from competitors and predators. I further hypothesized that social interactions with other fishes would occur more frequently than expected in the peripheral regions of the home range areas. The only prediction that was largely supported was that core use areas provide refuges from agonistic encounters with damselfish.

Behaviours within activity centers

Evidence for single and multiple activity centers within larger areas of movement has been found in other fishes (Warden and Lorio 1975, Nursall 1977, Gerking 1994, Bradbury et al. 1995, Coleman and Wilson 1996, Chilton and Poarch 1997, Zeller 1997). Some studies have characterized the behaviours within these activity centers; however, no common trends exist among these few studies. Feeding has been found to occur at a higher frequency in the core use areas within home ranges of juvenile pumpkinseed sunfish, *Lepomis gibbosus* (Coleman and Wilson 1996), whereas feeding occurred both peripherally and centrally in the goby, *Coryphopterus nicholsi* (Cole 1984). The distribution of aggressive acts within home range areas is also not consistent among fishes that have been studied. Cole (1984) found that aggressive events occurred mainly on the periphery of areas of activity for *C. nicholsi*. Similarly, Matsumoto et al. (1999) found that aggression between two temperate labrids, *Pseudolabrus eoethinus* and *P. sieboldi*, usually occurred near the border of the participants' home ranges. However, Coleman and Wilson (1996) found that *L. gibbosus* are not restricted to their home ranges by intraspecific aggression, and aggression did not vary as a function of location within their home ranges. This study addressed the questions of whether or not 1) feeding and solitary behaviour occurred more often in central areas of activity, and 2) encounters with aggressive interspecific competitors (i.e. damselfish) occurred less often in these activity centers.

I found differences in behavioural frequencies and differences in the distribution of behaviours throughout home ranges among these labrids. *Halichoeres bivittatus* and *H. maculipinna* showed a higher frequency of eating and eating + touching nose to the substrate than the other species. *Halichoeres bivittatus* showed a higher frequency than expected eating in their core use areas than in the other parts of their home ranges. *Halichoeres garnoti* also showed a higher frequency than expected eating + touching nose to the substrate in the core use areas of their

home ranges. However, *H. maculipinna* displayed a random distribution of eating and eating + touching nose to the substrate throughout their home ranges, and *Thalassoma bifasciatum* showed a higher frequency than expected eating + touching nose to the substrate in the middle regions of their home ranges. Therefore, my hypothesis that feeding would be more frequent in the activity centers than peripheral regions was only supported by *H. bivittatus* and *H. garnoti*.

A second behaviour that I hypothesized would be performed more frequently in the central regions of home ranges was swimming alone. This hypothesis was based on the assumption that core use areas would serve as refuges from predators and aggressive competitors, and that being solitary is a “riskier” behaviour than being with others (Cowlshaw 1999). Although *H. bivittatus* showed a higher frequency of swimming alone than any other species except *H. poeyi*, all species performed this activity randomly throughout their home ranges.

In contrast to swimming alone and eating, I hypothesized that agonistic encounters with damselfish would occur less often in the core use areas than the peripheral regions of the home range. This hypothesis is also based on the assumption that core use areas should provide refuges from aggressive competitors. Overall, *H. bivittatus* showed a lower number of agonistic occurrences with damselfishes than the other species. However, all species except *Halichoeres maculipinna* (which showed a non-significant trend), showed fewer damselfish chases than expected in the core use areas, and more than expected in the peripheral regions of home ranges. Individual *Halichoeres bivittatus* and *H. garnoti* both showed heterogeneous distributions of this behaviour compared with conspecifics. All *H. poeyi*, all *T. bifasciatum*, 59 % of *H. bivittatus*, and 64 % of *H. garnoti* showed non-random distributions of agonistic encounters with damselfish, and the distribution was skewed towards more interactions than expected in the peripheral regions. This significant effect of damselfish on the distribution of behaviours within home range areas, and the potential subsequent effect on home range shape and position was not surprising. Many studies

have investigated the effects of damselfish on the behaviour of other coral reef fishes (Low 1971, Keenleyside 1972, Katzir 1981, Hourigan 1986, Risk 1998).

Territorial damselfish direct their aggression towards conspecifics and heterospecifics (Thresher 1976, Katzir 1981), and some species (e.g. *Plectroglyphidodon biocellatus*, Keenleyside 1972) are less aggressive towards approaching conspecifics than towards small labrids, which are egg predators of many damselfish. These studies confirm that some damselfish are capable of discriminating between species, and vary their levels of aggression accordingly. Experimental removals of damselfish have resulted in increases in herbivorous fishes (Acanthuridae, Scaridae) within the territories once defended by damselfish (Low 1971, Sale 1974, Robertson et al. 1976, Hourigan 1986, Lawson et al. 1999). Damselfish removals also resulted in a shift from schooling behaviour to defense of small areas in the acanthurid, *Acanthurus nigrofusus*, and a transition of nighttime feeding to daytime feeding in the chaetodontid, *Chaetodon quadrimaculatus* (Hourigan 1986). Another acanthurid study by Risk (1998) found that post-settlement persistence in *Acanthurus bahianus* was negatively related to the level of aggression received from damselfish. In contrast, Green (1992) found higher densities of labrid and scarid recruits within damselfish territories because the recruits are attracted to the stands of macroalgae that are restricted to these territories. However, that pattern was not observed in this study. The distribution of algal turf may be different at Green's study site at Lizard Island, Great Barrier Reef, from the Caribbean site in the present study. In related work (Chapter VI), I introduced damselfish into home ranges of *H. bivittatus*, and showed that damselfish caused home range relocation in both juvenile and adult *H. bivittatus*, and a reduction in the amount of time adults spent either foraging or in a foraging assemblage. All of these studies suggest that the distribution of damselfish on coral reefs may significantly affect the spatial arrangements and behaviours of other families of reef fishes.

Behaviours in the peripheral regions of home range areas

Grouping behaviour leads to a reduction in the probability of predation (Bertram 1978, Magurran 1990), and other advantages including increased foraging in groups, and shared territory defense (Gross and McMillan 1981). The benefits of grouping behaviour should be similar between conspecific associations and heterospecific associations if species are similar in their vulnerability to predation and in efforts spent searching or probing for food (Coulson 1999). These labrids are morphologically similar, some species show similar colour patterns, and they are omnivorous, suggesting that the advantages may be the same for conspecific and heterospecific associations. I hypothesized that these fishes are more likely to swim with other fish or perform activities in close proximity to other fish in the peripheral regions of their home range areas. This hypothesis was based on the assumption that peripheral regions of home ranges may be “riskier” areas than the core use areas.

In general, *H. maculipinna* and *Thalassoma bifasciatum* showed a higher frequency of swimming with others than *H. garnoti* and *H. poeyi*. *Halichoeres maculipinna* also showed a higher frequency of doing activities in close proximity to others than the other species. In spite of these differences among the species with respect to social interactions, the only species that showed a non-random spatial distribution was *H. garnoti*. This species showed a higher frequency than expected swimming with others in the middle region of its home ranges. Contrary to my hypothesis, and despite its apparent importance to labrids (20 to 45% of their behaviours were performed while interacting with other fishes), interactions (both intra- and interspecific) appear to be occur randomly throughout their entire home ranges.

Concluding statements

To address behavioural mechanisms, we need to know whether social interactions vary with an individual's location within its home range and whether food distribution affects these interactions. The results of this study highlight the importance of interspecific interactions on the space use and local distribution of mobile animals. The presence or prior residence of territorial damselfishes on coral reefs might importantly modify the post-settlement selection of home range areas by these labrid species.

Table 4.1. Average area (m²) encompassed by the home range isopleths estimated using the adaptive kernel method (= AK) in CALHOME. TL = total length of fish (cm). The last column represents the ratio of core activity center (AK 30%) to home range area (AK 95%). Although the 30% isopleth encompasses 30% of the observation points, the area covered is based on the spread of the observation points and is not based on area. For example, the 30% core activity center for *Halichoeres bivittatus* only covers 8.3 % of the home range area. Numbers in all columns are mean with SE in parentheses.

SPECIES	n	TL	AK 30%	AK 75%	AK 95%	AK30 / AK95
<i>Halichoeres bivittatus</i>	44	11.4 (0.3)	3.61 (0.28)	15.52 (0.85)	32.70 (2.10)	0.083 (0.014)
<i>H. garnoti</i>	11	11.9 (0.2)	2.53 (0.029)	13.81 (2.42)	35.30 (7.70)	0.13 (0.018)
<i>H. maculipinna</i>	13	11.7 (0.5)	3.97 (0.81)	19.20 (3.47)	48.80 (9.50)	0.12 (0.013)
<i>H. poeyi</i>	14	10.7 (0.4)	2.44 (0.41)	11.25 (2.07)	26.50 (6.10)	0.16 (0.017)
<i>Thalassoma bifasciatum</i>	12	7.4 (0.3)	3.37 (0.38)	15.42 (1.52)	33.20 (3.30)	0.14 (0.011)

Table 4.2. Results of testing for a random distribution of activities throughout the home range area using the χ^2 goodness of fit (GOF) analysis. Before pooling individuals within a species, a heterogeneity χ^2 test determined whether the focal individuals represented a homogeneous sample (heterogeneity χ^2 vs. $\chi^2_{(\alpha=0.05)}$). If individuals within a species were homogeneous, one χ^2 test was performed on the data and indicated as reject/accept the null ratio in the last column. If individuals within a species were not homogeneous, separate χ^2 GOF tests were performed, and the numbers rejected/accepted are presented in the last column. The null ratio of 30:45:20 comes from the random distribution of points within the adaptive kernel isopleths (30% of the points between 0-30%, 45% between 30-75%, and 20% between 75-95%). Methods for the χ^2 heterogeneity tests and GOF tests are found in Zar (1996).

SPECIES	$\chi^2_{(\alpha=0.05)}$	ACTIVITY	Heterogeneity χ^2	Homogenous Sample?	Pooled/ Separate test(s); Accept/ Reject Null Ratio of 30:45:20? (At $p = 0.05$)
<i>H. bivittatus</i> n = 44	59.30	<i>eat</i>	55.28	yes; $p = 0.075$	pooled; reject
		<i>eat + touch nose to substrate</i>	79.22	no	separate; accept for all
		<i>chased by damselfish</i>	60.17	no	separate; reject for 26/44
		<i>swim alone</i>	71.58	no	separate; accept for all but 3
		<i>swim with others</i>	69.08	no	separate; accept for all
		<i>all activities with other fishes</i>	99.82	no	separate; accept for all but 2
<i>H. garnoti</i> n = 11	18.31	<i>eat</i>	11.36	yes; $p = 0.375$	pooled; accept
		<i>eat + touch nose to substrate</i>	9.23	yes; $p = 0.625$	pooled; reject
		<i>chased by damselfish</i>	32.72	no	separate; reject for 7/11
		<i>swim alone</i>	9.29	yes; $p = 0.625$	pooled; accept
		<i>swim with others</i>	9.05	yes; $p = 0.625$	pooled; reject
		<i>all activities with other fishes</i>	20.08	no	separate; accept for all but 4

Table 4.2. (Continued)						
SPECIES	χ^2 ($\alpha = 0.05$)	ACTIVITY	Hetero- geneity χ^2	Homogenous Sample?	Pooled/ Separate test(s); Accept/ Reject Null Ratio of	
<i>H. maculipinna</i> n = 13	21.03	<i>eat</i>	9.26	yes; p = 0.625	pooled; accept	
		<i>eat + touch nose to substrate</i>	12.30	yes; p = 0.375	pooled; accept	
		<i>chased by damselfish</i>	23.51	no	separate; accept for all but 4	
		<i>swim alone</i>	8.72	yes; p = 0.625	pooled; accept	
		<i>swim with others</i>	33.98	no	separate; accept for all but 3	
		<i>all activities with other fishes</i>	28.14	no	separate; accept for all	
<i>H. poeyi</i> n = 14	22.36	<i>eat</i>	21.15	yes; p = 0.075	pooled; accept	
		<i>eat + touch nose to substrate</i>	33.21	no	separate; accept for all	
		<i>chased by damselfish</i>	10.45	yes; p = 0.625	pooled; reject	
		<i>swim alone</i>	14.08	yes; p = 0.375	pooled; accept	
		<i>swim with others</i>	26.65	no	separate; accept for all but 2	
		<i>all activities with other fishes</i>	21.04	yes; 0.075	pooled; accept	
<i>T. bifasciatum</i> n = 12	19.67	<i>eat</i>	27.27	no	separate; accept for all but 2	
		<i>eat + touch nose to substrate</i>	10.38	yes; p = 0.625	pooled; reject	
		<i>chased by damselfish</i>	13.14	yes; p = 0.175	pooled; reject	
		<i>swim alone</i>	24.57	no	accept for all but 2	
		<i>swim with others</i>	18.40	yes; p = 0.075	accept	
		<i>all activities with other fishes</i>	31.43	no	accept for all but 3	

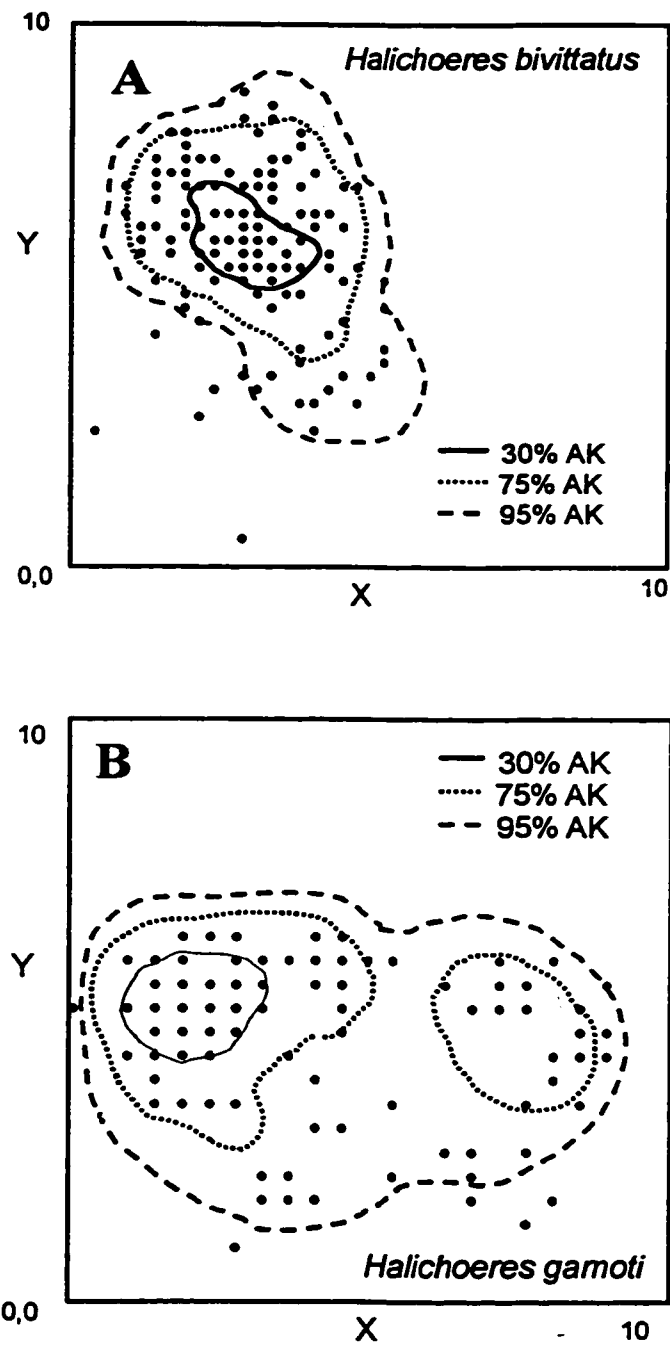


Figure 4.1. Distribution of observation points for two representative focal individuals.

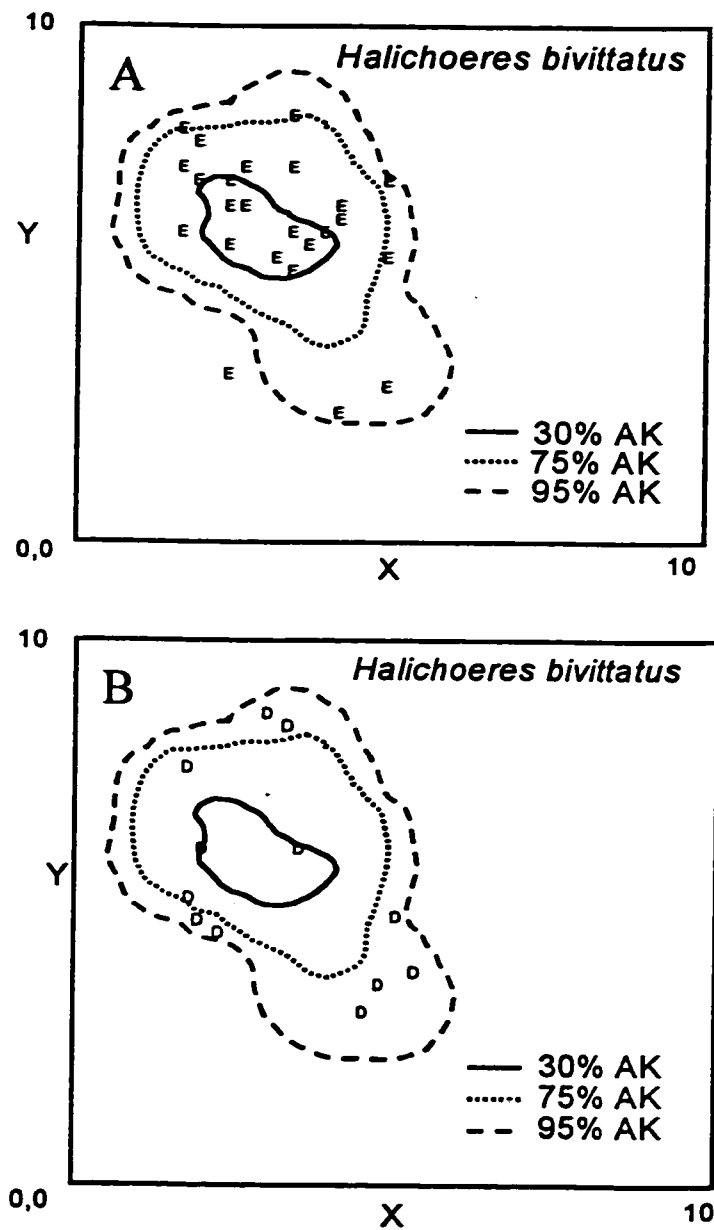


Figure 4.2. An example showing the distribution of behaviours over the adaptive kernel isopleths of a focal *Halichoeres bivittatus* ($n = 120$). Panel A shows those points where the individual ate or bit at the substrate (= E), and Panel B shows those points where agonistic encounters with pomacentrids occurred (= D).

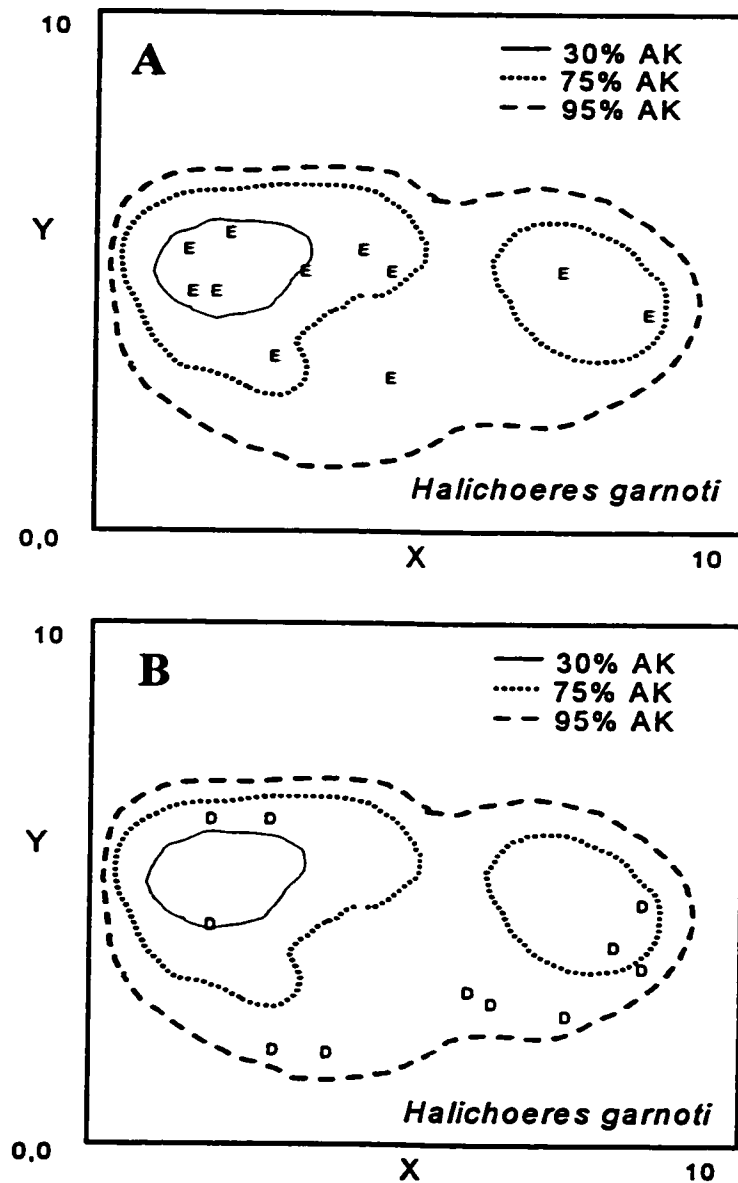


Figure 4.3. An example showing the distribution of behaviours over the adaptive kernel isopleths of a focal *Halichoeres garnoti* (n = 120). Panel A and B are similar to those of Fig. 4.2. Note that the adaptive kernel isopleths delineates one core use area, but two activity areas within the 75% isopleth for this particular individual.

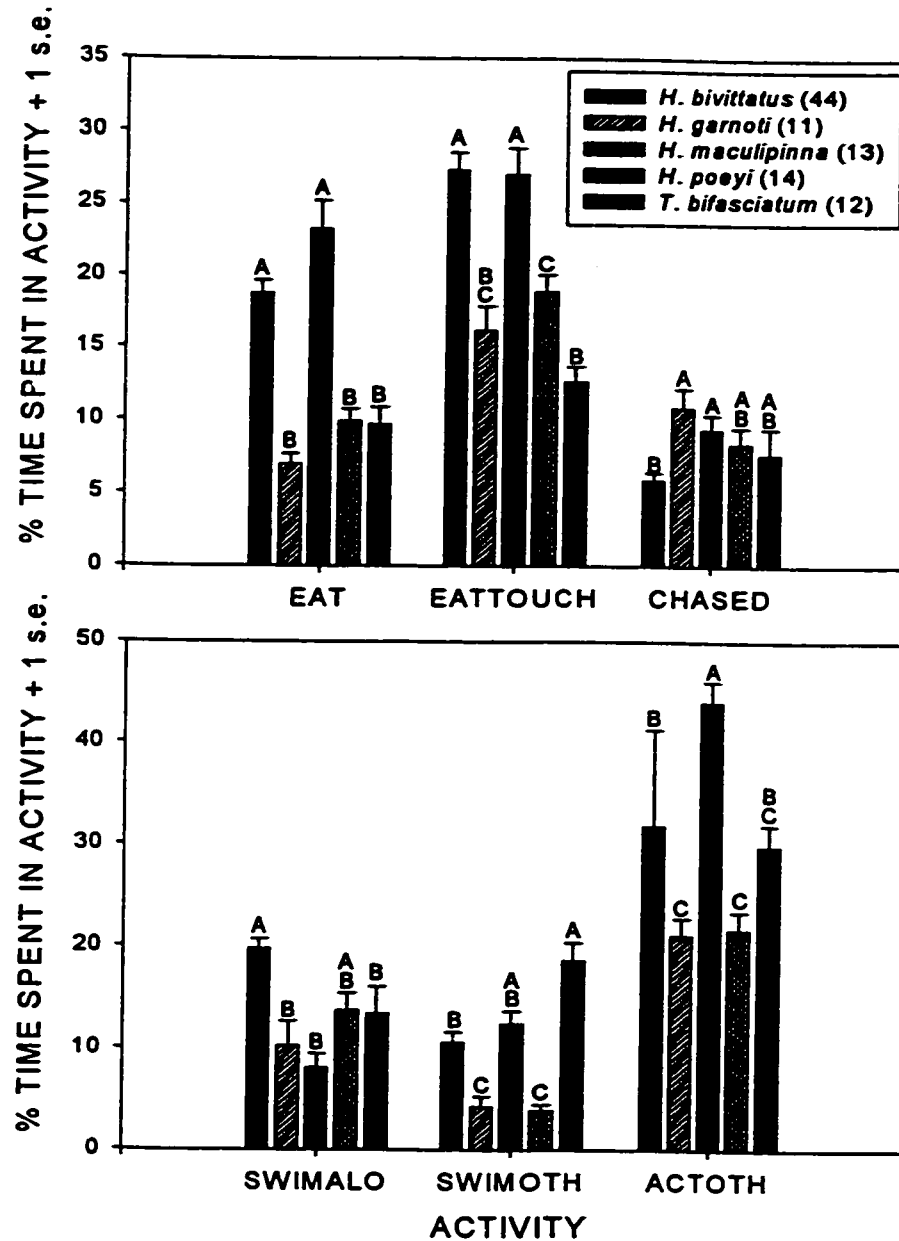


Figure 4.4. Frequency of observations of common labrid behaviours. EAT = eating or biting the substrate, EATTOUCH = eating or biting the substrate + touching nose to the substrate, CHASED = being chased by a pomacentrid, SWIMALO = swimming alone, SWIMOTH = swimming with conspecifics or heterospecifics, ACTOTH = any activity performed with other fishes < 2 body lengths away from the focal individual. The results from a one-way ANOVA among species but within each activity are represented by the letters above the bars. If two bars within an activity share the same letter, they are not significantly different at the level of $p < 0.05$. The ANOVA were performed on angular transformed data, although the data graphed are untransformed percentages.

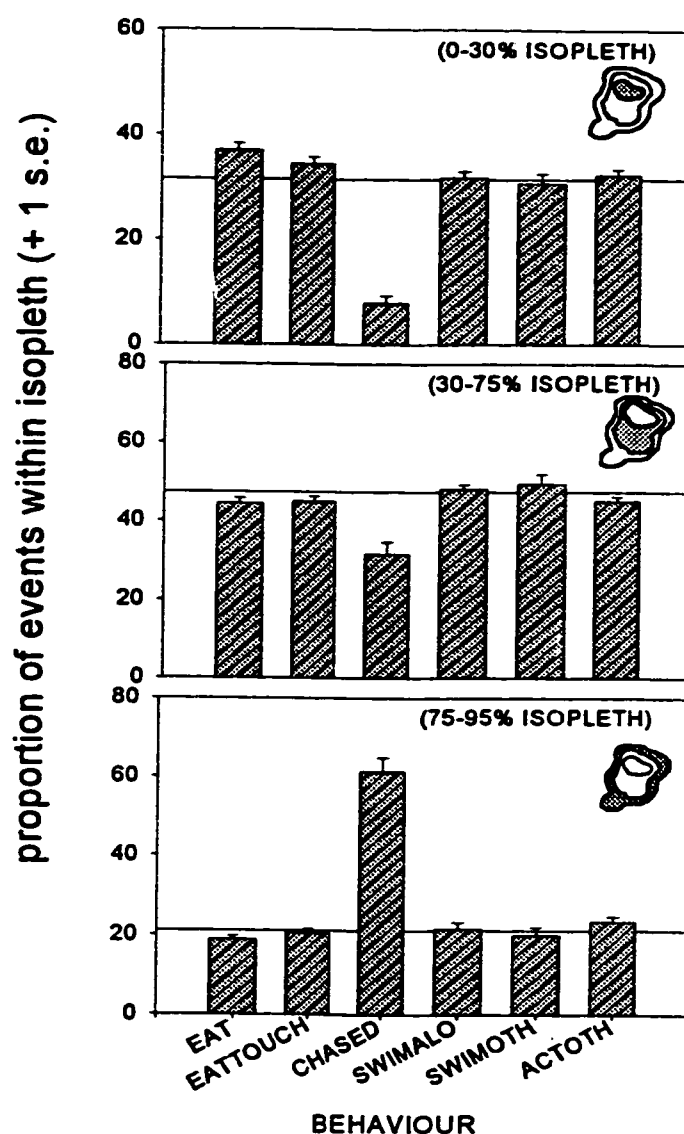


Figure 4.5. Proportion of occurrences of particular activities within each isopleth of home range of *Halichoeres bivittatus*. The lines represent the expected percentage if the activity was performed randomly throughout the home range area. The top panel represents the core use area, or that area encompassed by the 30% adaptive kernel (AK) isopleth, the middle panel represents the area encompassed between the 30% AK isopleth and the 75% AK isopleth, and the bottom panel represents the peripheral home range contour, or the area encompassed between the 75% AK isopleth and the 95% AK isopleth. Bars that are above the expected frequency line indicate that activity was performed more than expected at random within that particular isopleth. These data are analyzed with the chi-square goodness of fit method presented in Table 2. The abbreviations for the activities are the same as those used in Fig. 4.4. (n = 44)

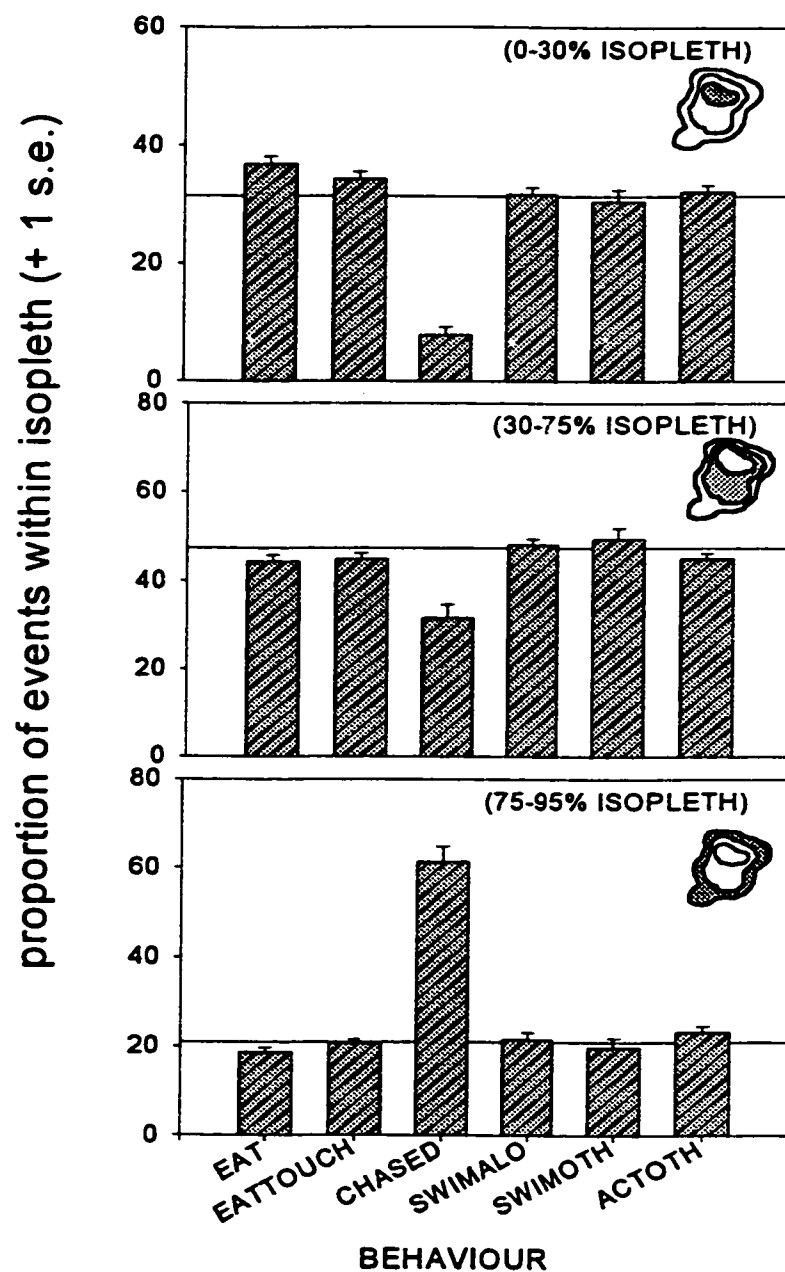


Figure 4.6. Distribution of activities for *Halichoeres garnoti*. The explanation is the same as in Figure 4.4. (n = 11)

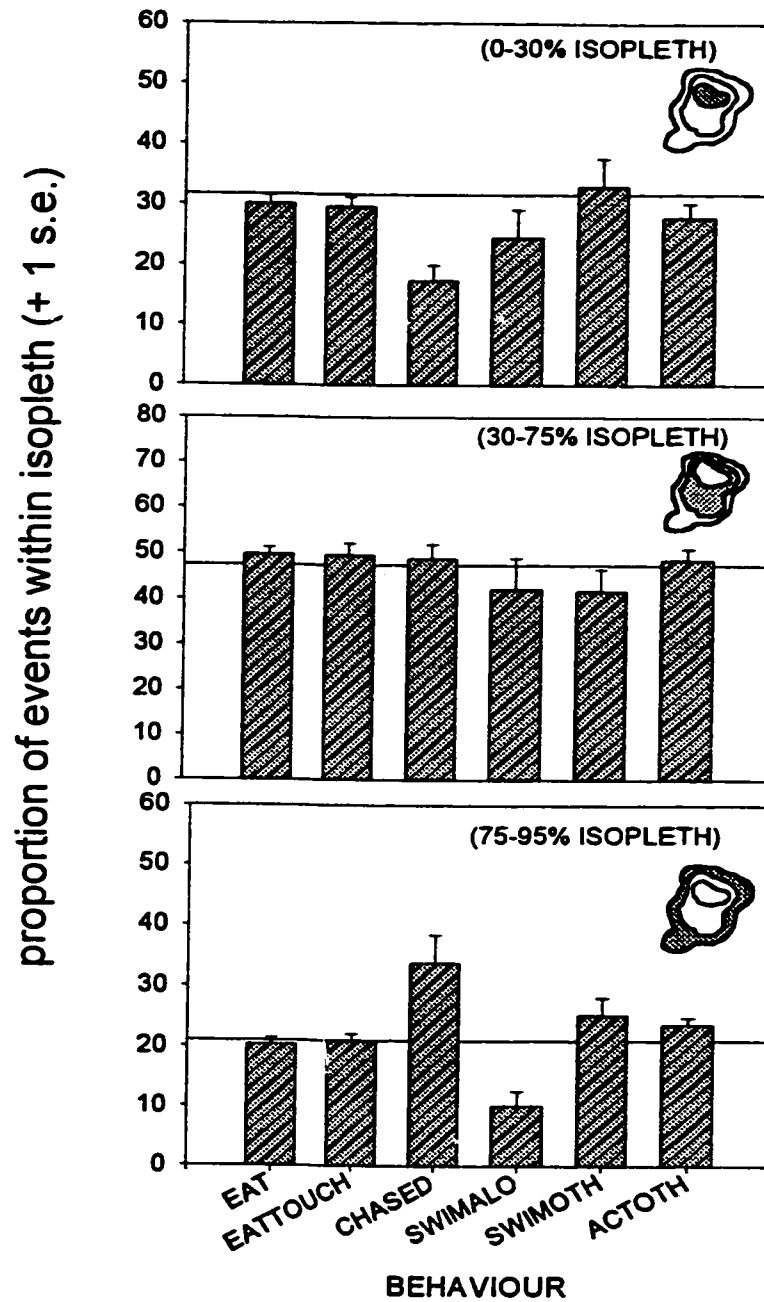


Figure 4.7. Distribution of activities for *Halichoeres maculipinna*. The explanation is the same as in Fig. 4.4. (n = 13)

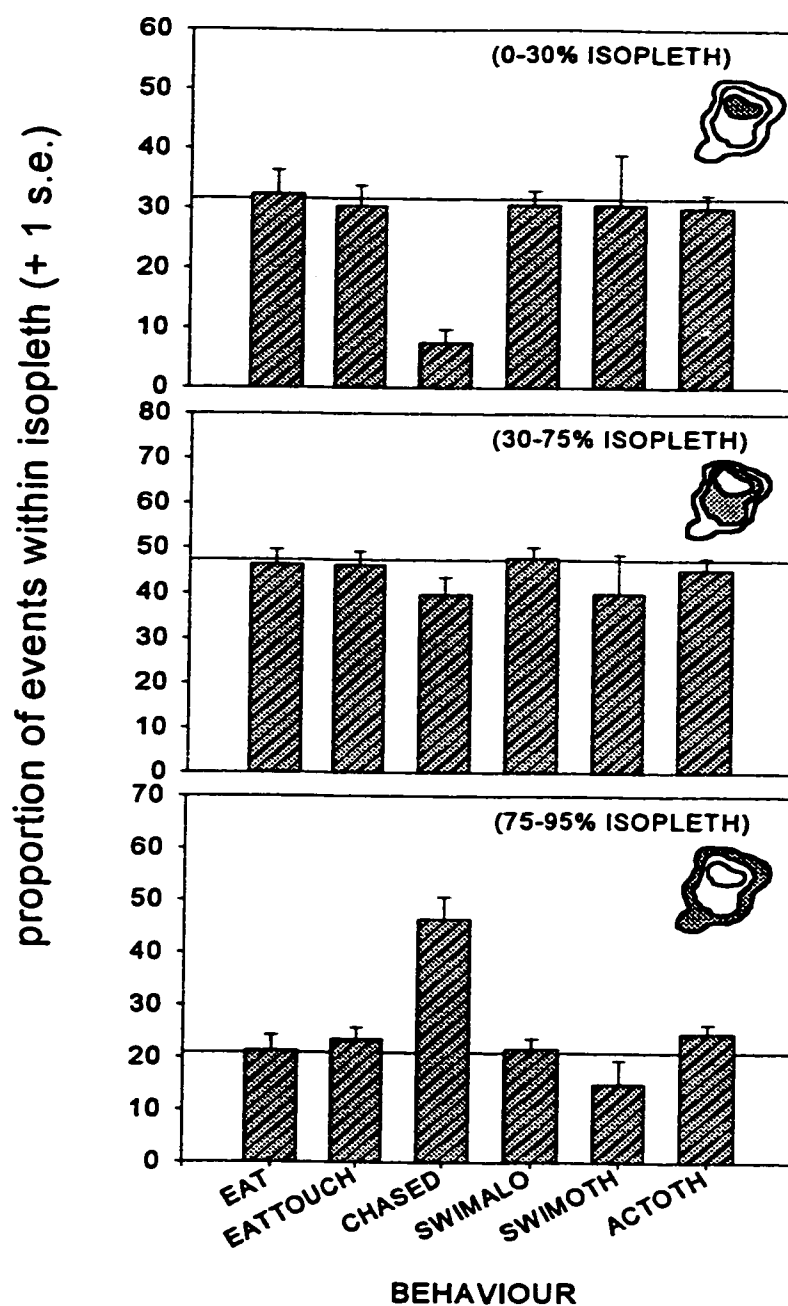


Figure 4.8. Distribution of activities for *Halichoeres poeyi*. The explanation is the same as in Fig. 4.4. (n = 14)

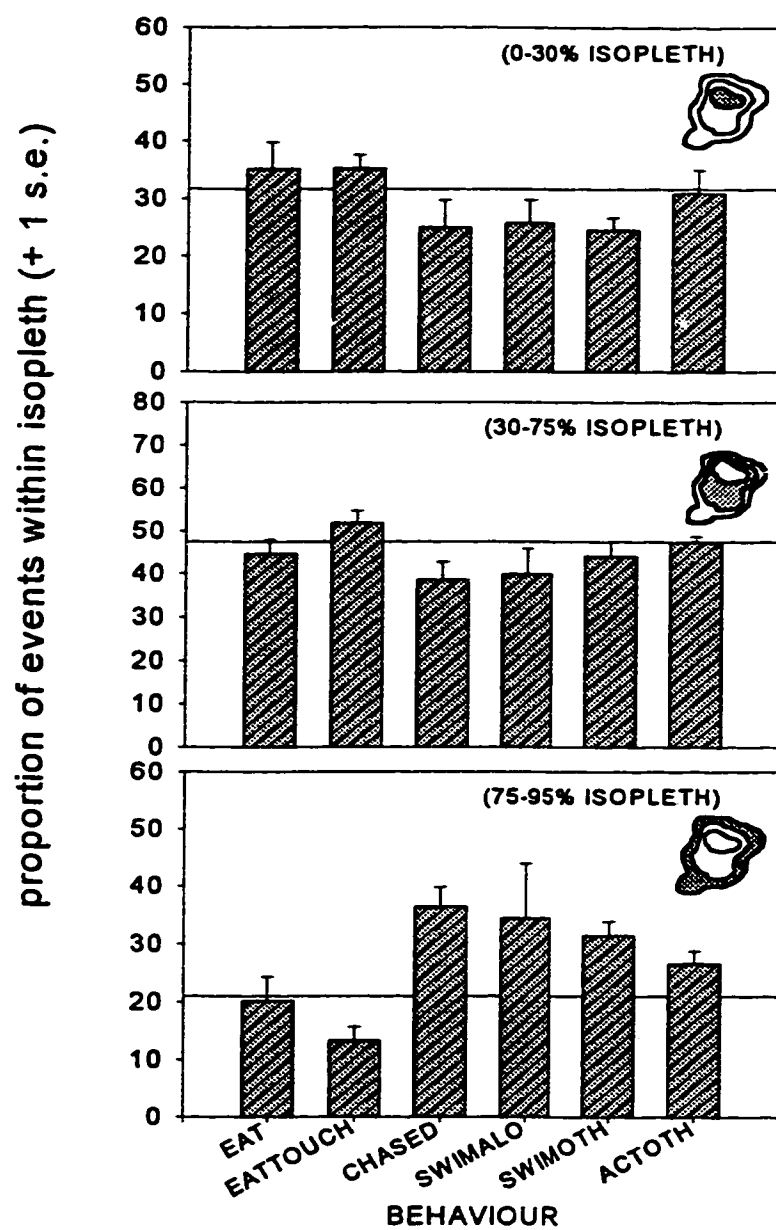


Figure 4.9. Distribution of activities for *Thalassoma bifasciatum*. The explanation is the same as in Fig. 4.4. (n = 12)

CHAPTER V

ONTOGENETIC SHIFTS AND OVERLAP IN MICROHABITAT USE AMONG SIX CARIBBEAN LABRID SPECIES

ABSTRACT

This study examines the use of microhabitats by six ecologically similar coral reef fishes (family Labridae), including *Halichoeres bivittatus*, *H. garnoti*, *H. maculipinna*, *H. poeyi*, *H. radiatus*, and *Thalassoma bifasciatum*. Previous studies have shown high dietary and behavioural overlap among the species. However, there are few studies examining the degree of ontogenetic and interspecific microhabitat overlap in these labrids. In this study, three methods of quantifying microhabitat use were used: 1) percent area coverage of microhabitats within fish-occupied quadrats, 2) 5- min behavioural observations that simultaneously recorded the microhabitat in closest proximity, and 3) four sets of 10-min repeated behavioural observations on focal individuals within their home range areas in which microhabitat availability was estimated. A high degree of variability in microhabitat use within life stages and species was observed, and discriminant function analyses of the data sets yielded poor classification of group membership (life stage and species). Despite this, there were consistent interspecific and ontogenetic differences. For example, all life stages of *Halichoeres bivittatus* (juveniles, initial phase, and terminal phase adults) prefer less topographically complex microhabitats, including sand and pavement (= coralline limestone bench). All life stages of *Halichoeres poeyi* commonly use algal habitats at higher frequencies than the other species, and *Thalassoma bifasciatum* commonly show a preference for *Porites porites* rubble. Ontogenetically, there also were consistent

differences in microhabitat use. All species showed increasing preference for less topographically complex microhabitats as they develop from juveniles into initial phase and terminal phase adults. Overall, some of these labrid species were more similar in terms of microhabitat preferences with heterospecifics of the same life stage than they were with conspecifics of different life stages.

INTRODUCTION

The distribution of a species may be determined by the behaviour of individuals selecting habitats. Small-scale movements of animals with respect to habitat can have important consequences for a species and its interactions with surrounding resources and other members of the local community. Despite its obvious importance, habitat selection is one of the most poorly understood ecological processes (Krebs 1995). Animals select habitats for various reasons, including food resources (Keast and Webb 1966, Love and Ebeling 1978, Jones 1986, McCormick 1994), spawning sites (Fricke 1975, Walsh 1987, Danilowicz 1995, Warner 1995), nesting sites (Fretwell and Lucas 1970, Moller 1991, Brandt et al. 1995), sleeping sites (Robertson and Sheldon 1979), protection from predation (Hall and Werner 1977, Holbrook et al. 1990, Shulman 1985a, Jones 1988a, Lemmens et al. 1990, Tabor and Wurtsbaugh 1991, Anderson 1994), and protection from stressful environmental conditions (e.g. extreme temperatures (Cowie 1985, Jones and Boulding 1999), or wave action (Boulding and VanAlstyne 1993)). Habitat characteristics are so fundamental to the evolution and ecology of the organisms that habitat use has been proposed as the basis for a variety of ecological classifications of organisms, including fishes (Balon 1975). Indeed, demersal tropical fish species can often be categorized according to habitat and depth preferences (Sale 1980, Jones 1988a, Adjerdoud et al. 1998, Jones and Syms 1998, Tolimieri 1998).

Coral reef fishes are members of highly diverse assemblages, and it was early hypothesized that niche diversification in either dietary or habitat resources facilitated their high diversity (Smith

and Tyler 1972, 1973a,b, 1975, Ehrlich 1975, Goldman and Talbot 1976, Smith 1978, Sale 1980, Jones 1991). However, several investigations have since revealed that chance events, i.e. the unpredictable recruitment of coral reef fishes, often have a larger effect on the types of species and the number of individuals that are found on suitable reef habitat (Sale 1974, 1977, 1978b, 1980, Russell et al. 1974, Ehrlich 1975, Williams 1980, Doherty 1983, Doherty and Williams 1988, Jones 1990). Regardless of chance events that may assemble fish species on a coral reef, once fish recruits arrive, their reliance on reef resources (i.e. food, habitat, and presence of potential mates) is indisputable. Species that are closely related and ecologically similar require similar resources (food and habitat), and exploit those resources in similar ways. This study investigates microhabitat use in six sympatric reef fish species (family Labridae), and assesses the degree of similarity among life stages and across the species. These labrids are commonly found together in the same habitats (i.e. reef zones) and microhabitats (i.e. homogeneous patches of substrate types or coral species) foraging together with minimal agonistic encounters.

Whether or not species segregate by habitat depends on the species in question, the spatial scale of the study, and the methods of habitat quantification. Reef fish species tend to be reliably distributed according to habitat type at spatial scales of 10-100 meters (Sale 1991a). At a smaller spatial scale, that of the microhabitat, the situation is less clear. Different studies in the same systems (e.g. patch reef assemblages (Sale and Douglas (1984) versus Gladfelter et al. (1980)); or territorial pomacentrids (Sale (1974) versus Robertson and Lassig (1980))) have found contrasting results. Sale (1991a) states that the dissimilar findings can be explained either by the spatial scale of the study, or the method of habitat quantification. Ecologists must exercise caution when considering these factors, in order to reduce anthropocentric perceptions of habitat use, and to reduce the tendency to use sampling methods of convenience. In the present study, three different methods of quantifying microhabitat use were employed. Additionally, part of this study was

conducted after spatial requirements of these labrids were quantified (i.e. home range area - see Chapter 1) in order to use an appropriate spatial scale of study.

By providing refuges, habitat structure may mediate the outcome of biological interactions, such as competition and predation (Jones 1988b, Connell and Jones 1991, Hixon and Menge 1991, Hixon and Beets 1993, Caley and St. John 1996). Jones (1991) has drawn attention to the role of habitat structure in modifying post-recruitment processes such as predation and competition. Despite this, little is known about the mechanisms by which habitat structure influences assemblage structure of reef fish (Jones 1991), and these interactions have not played a major role in the development of ecological theory regarding this group of organisms (Sale 1991b).

Reef fishes commonly undergo ontogenetic changes in resource use, including diet (Bellwood 1988, Harmelin-Vivien 1989), and habitat (Shulman and Ogden 1987, Harmelin-Vivien 1989, Lirman 1994, McAffe and Morgan 1996, Green 1996). For the majority of tropical marine fish, there appears to be a decrease in the relative importance of microhabitat structure for older, larger fish relative to postsettlement larvae, recruits, and juveniles (e.g. many damselfishes (Pomacentridae)(Clarke 1977, Itzkowitz 1977a, Waldner and Roberston 1980, Lirman 1994)). More conspicuous ontogenetic shifts in habitat have been documented for larger, more mobile reef fishes (e.g. groupers (Serranidae), snappers (Haemulidae), and grunts (Lutjanidae)), that often settle in seagrass habitats and then migrate to reef habitats when they reach a certain size or age (e.g. Smith and Tyler 1975, McFarland 1979, Brothers and McFarland 1981, Parrish 1987, Eggleston 1995, Sluka and Sullivan 1996). Few studies have looked at ontogenetic shifts in labrid species. In one study, only two of eight labrids studied by Green (1996) on the Great Barrier Reef showed ontogenetic changes in microhabitat use between recruits and adults.

The Caribbean labrids in this study (*Halichoeres bivittatus*, *H. garnoti*, *H. maculipinna*, *H. poeyi*, *H. radiatus*, and *Thalassoma bifasciatum*) have been the focus of many ecological

studies (e.g. Roede 1972, Warner et al. 1975, Warner and Robertson 1978, Thresher 1979, Robertson 1981, Wainwright 1988). However, microhabitat overlap among juvenile, initial phase, and terminal phase conspecifics, and among heterospecifics has never been closely investigated. These sympatric labrids are demersal, site-attached fishes in which conspecific life stages and heterospecifics extensively overlap and interact within reef habitats. This study addresses two specific questions: 1) Within these habitats, are microhabitats partitioned in any way among the different species, or do they show random microhabitat use? 2) Do juveniles prefer more sheltered microhabitats than adults?

METHODS

Study animals

Juveniles, initial phase adults (IP), and terminal phase adults (TP) of the following labrid species were studied: *Halichoeres bivittatus*, *H. garnoti*, *H. maculipinna*, *H. poeyi* and *Thalassoma bifasciatum*. *Halichoeres radiatus* juveniles were included, but adults are much larger and more mobile than the other life stages and species so they were excluded from this study. There is considerable difference in color among these labrids as well as among the life stages within species. Colour pattern often provided a good indication of life stage within these species (Roede 1972, Warner and Robertson 1978). Juveniles and IP adults are easily distinguishable for *H. garnoti* and *H. radiatus*. For *H. bivittatus*, *H. maculipinna*, *H. poeyi*, and *Thalassoma bifasciatum* juveniles were $\leq 30\text{mm}$ in total length (c.f. Warner and Robertson 1978). Terminal phase adults were easily distinguished from IP adults in all of the species because of their bolder colour patterns (except *Halichoeres poeyi*), and changes in morphology.

Study Site

The present study was conducted on Tague Bay reefs, along the northeastern coast of St. Croix, U.S.V.I. (17°36'N, 64°36'W). Algae growing on coral rubble (algal turf) was the predominant substratum, followed by dead *Porites porites*, dead *Acropora palmata*, other small, broken pieces of dead coral, and sand. Other live corals such as *Siderastrea* spp., *Diploria* spp., and *Agaricia* spp., and a variety of small coral heads, as well as gorgonians, sponges, and seagrass beds (mostly *Thalassia testudinum*) occurred but were less common. The back reef of this bank barrier reef drops off to a sandy lagoon floor at ~ 5m depth. The main seagrass in the lagoon is *Thalassia testudinum*. *Syringodium filiforme* and *Halodule wrightii* are also observed in smaller amounts. The first two phases of this study was carried out during May-August 1997, and the third phase was carried out during May-August 1998 and 1999.

Habitat Quantification

Microhabitat categories were consistent throughout the three phases of this study. The following microhabitats were categorized: 1) *Acropora palmata* rubble, 2) live *Porites porites*, 3) *Porites porites* rubble, 4) live *Montastrea annularis*, 5) *Montastrea annularis* rubble, 6) algae growing on coral rubble, 7) algae or isolated seagrass blades surrounded by sand, 8) small, unidentifiable pieces of coral rubble, 9) other live coral species, 10) gorgonians, 11) sea fans, 12) sponges, 13) sand, 14) "pavement" (= hardened, planar surfaces of dead coral sometimes covered in a thin layer of sand), 15) live *Porites astreoides*, 16) *Agaricia* species, 17) live *Millepora complanata*, 18) live *Siderastrea siderea*, 19) *Diploria* species, 20) seagrass (most commonly *Thalassia testudinum*), and 21) other microhabitats.

Study I: Percent area coverage of fish- occupied quadrats

This preliminary study investigated general microhabitat differences between juveniles and IP adults within species, and microhabitat differences among species. Prior to collecting data on individuals, a randomized order of species and life stages was preset on an underwater slate. As individuals that fulfilled the criteria were encountered while SCUBA diving along continuous back- and fore- reef habitat, 1 m² quadrats were placed on the substrate with an individual fish situated in the centre of the quadrat. The quadrat was divided into 25 cells (20x20 cm), and the dominant microhabitat was recorded for each cell. Null quadrats were used to quantify the average availability of microhabitats. The null quadrats may or may not have had fish present. They were systematically placed every five kick cycles along 100m transects used in another study (Chapter VII). Approximately 50 fish-occupied quadrats per life stage and species were quantified, and 256 null quadrats were quantified (for a total of 833 quadrats). Juveniles and IP adults were studied for all species except *H. radiatus*, which was excluded from this particular investigation.

Study II: Records of microhabitat use during 5-minute behavioural observations

This second study concurrently recorded microhabitat use while investigating behaviour. Similar to the first study, prior to collecting data on individuals, a randomized order of species and life stages was preset on an underwater slate. As individuals that fulfilled the criteria were encountered, I began behavioural and microhabitat observations after two minutes of following the focal fish (to allow for acclimation by the fish to the observer). If the required individual was not found within three minutes of searching, I went on to the next individual in the list. I followed each individual for five minutes, and recorded behaviours and the microhabitat in closest proximity to the focal individual every 10 seconds, for a total of 30 observations per individual. Juveniles and IP adults from all species were studied, with the exception of *H. radiatus*, for which only juveniles were included. A total of 249 individuals were observed, with a minimum of 11 individuals per life

stage.

Study III: Records of microhabitat use during 4 sets of 10- minute behavioural observations

The first study provided a “snapshot” of microhabitats within 1m² areas surrounding focal fish. The second study revealed the microhabitats in closest proximity to focal fish while they moved around the reef, with no quantification of microhabitat availability. It also revealed high variability in microhabitat use among conspecifics, which could have been explained by random movements over patches of microhabitat. This third study followed individuals repeatedly over a period of up to two weeks in order to reduce variability in microhabitat use within an individual fish, and to better quantify microhabitat availability within the vicinity of the focal fish. During the first two studies, I made qualitative observations of different patterns of distribution of TP individuals compared with juveniles and IP adults, so TP fishes were included in this study. This study included juvenile *H. radiatus*, and juveniles, IP, and TP adults for the other five species.

Initially in 1998, individual fishes of all species were caught with a lift net (see Roede 1972) and tagged with beaded Floy® tags to verify the sedentary nature of these labrids. The fishes were anaesthetized with clove oil prior to tagging (Munday and Wilson 1997). The fishes quickly regained consciousness and resumed normal behaviours. After these preliminary investigations, I found that individual labrids could be reliably identified without catching and tagging by recognizing differences in facial markings, lateral line deformities, and/or size differences.

Quadrats (10x10 m²) were haphazardly marked on the reef with flagging tape. The habitat features of each quadrat were mapped on a slate. Mylar film was then placed over the map to record the positions of an individual fish during each observation period. Observations occurred between 0800 hr and 1500 hr, which appeared to be the peak activity periods for labrids on the reef. Observation periods were aborted if the focal individual was involved in a spawning episode

(which often occurs outside of the normal home range area). Observations were also not carried out on days when visibility fell below 10m (during storm events or algal blooms), because the fish were behaving abnormally. Individual fishes were randomly selected from each quadrat for observation. Each observation period lasted for 10 minutes, and at every 20 second interval, several aspects of the position (microhabitat use, swimming distance above the substrate), social interactions, and the behaviour of that fish were recorded (for a total of 30 points per observation period). The observation periods were pooled for each individual to get a better assessment of daily activities (the time of day was randomized for repeated observations). In a preliminary study, I found that an additional set of observations did not affect the size of the home range area estimated from four sets (Mann Whitney $T = 986.00$; $p = 0.812$). Thus, only four sets of observations were conducted on all subsequent focal individuals. The spatial coordinates and behaviours were analysed in chapters II, III, and IV. A total of 196 individuals were included in this study. A minimum of 11 juveniles, 11 IP adults, and 3 TP adults were observed for each species. Eleven *Halichoeres radiatus* juveniles were included.

Microhabitat Use: Microhabitat Availability Plots

In order to determine whether or not individuals (instead of groups) of each life stage and species are simply using microhabitats that are randomly positioned in close proximity to focal fish, microhabitat use: availability plots were constructed from the data collected in study III. For the eight most common microhabitats, the percent use of the microhabitat by each focal fish was plotted against the proportional availability of that microhabitat in the large (10x10m) quadrats in which the focal fish resided.

Statistical analysis

To determine if group membership can be predicted from microhabitat use, discriminant function analysis (DFA) was performed on the data from all three studies (Tabachnik and Fidell

1989, Morrison et al. 1992). Discriminant function analysis also reveals the degree of difference among groups (i.e. species and life stage) with respect to the predictor variables (in this case, the microhabitats). The DFAs were performed using the DISCRIM model in SYSTAT 8.0 software.

Study I:

In the first study, the predictor variables were the percent area coverage of microhabitats within fish-occupied quadrats. Percent area coverage of the microhabitat in each quadrat was angular transformed prior to analysis to improve normality and homogeneity of variances. Eight microhabitats were included in the analysis, and criteria for inclusion were based on $\geq 2.5\%$ area coverage within quadrats and presence in $\geq 24\%$ of the quadrats. The eight microhabitats included in the DFA in order of decreasing availability were: algae on coral rubble, *Porites porites* rubble, small coral rubble, *Acropora palmata* rubble, sand, algae or seagrass blades in sand, pavement, and live *Porites porites*.

Study II and Study III:

In the second and third studies, the predictor variables were the percent occurrences of labrids in each of the microhabitats. Percent occurrence in each microhabitat was angular transformed prior to analysis to improve normality and homogeneity of variances. Eight microhabitats were included in the analysis, and criteria for inclusion was based on $\geq 5\%$ of the occurrences. For the second study, the eight microhabitats included in the DFA (in decreasing percent occurrence) were: algae on coral rubble, *Porites porites* rubble, *Acropora palmata* rubble, sand, live *Montastrea annularis*, live *Porites porites*, algae on sand, and small coral rubble. For the third study, the eight microhabitats included in the DFA (in decreasing percent occurrence) were: algae on coral rubble, sand, algae on sand, algae on *Acropora palmata* rubble, *Montastrea annularis* rubble, pavement, and live *M. annularis*.

RESULTS

The most common and most frequently used microhabitat is algae on coral rubble (Fig. 5.1a, 5.2a, 5.3a). Most life stages and species use this microhabitat on an availability basis¹, with the exception of *Halichoeres poeyi*. In all of the studies, juveniles and IP adults of this species use algae on coral rubble more than the other species and at frequencies higher than availability. In the third study, however, *H. maculipinna* also uses this microhabitat at higher frequencies than the other species.

Study I

The first study method (Fig. 5.1a - h) revealed differences between life stages and among the species. For example, the most striking differences between life stages are for 1) *Porites porites* rubble (Fig. 5.1c), and 2) pavement microhabitats (Fig. 5.1f). First, *Thalassoma bifasciatum* juveniles are found in 1m² quadrats with higher percent area coverage of *P. porites* than conspecific adults. Second, juveniles of all species are found in quadrats with lower percent area coverage of pavement microhabitats than adult conspecifics.

The largest differences among species (additional to differences in use of algae on coral rubble (Fig. 5.1a)), are in the percent area coverage of the following microhabitats: *P. porites* rubble (Fig. 5.1c), sand (Fig. 5.1e), algae in sand (Fig. 5.1g), and live *P. porites* (Fig. 5.1h). *Thalassoma bifasciatum* are more commonly found in *P. porites* microhabitats than the other species; whereas the other four species are more commonly found in sand and algae on sand than *T. bifasciatum*. The four species (*H. bivittatus*, *H. garnoti*, *H. maculipinna*, and *H. poeyi*) are found in quadrats with higher percent coverage of sandy microhabitats than the availability in null

¹ Availability basis is defined as the proportional availability of that microhabitat. For example, if microhabitat X is available as 20% area coverage and species Y exhibits 20% use of that microhabitat, then species Y uses microhabitat X on an availability basis.

quadrats.

Study II

In agreement with study I, the second study also revealed differences between life stages and among the species, but there was no basis of comparison with microhabitat availability (Fig. 5.2a - h). This study method also had higher levels of variability than the other two methods. The largest differences between life stages were found in live *Acropora palmata* rubble (Fig. 5.2c), live *Montastrea annularis* (Fig. 5.2e), *P. porites* (Fig. 5.2f), and small coral rubble (Fig. 5.2h). Juvenile *H. maculipinna* and *T. bifasciatum* show higher use of live *P. porites* than adult conspecifics. *Halichoeres garnoti* adults show higher use of live *M. annularis* than juvenile conspecifics. *Halichoeres poeyi* juveniles show higher use of *A. palmata* rubble and small coral rubble than adult conspecifics.

The largest differences among species are in the frequency of use of *P. porites* rubble (Fig. 5.2b), sand (Fig. 5.2d), live *P. porites* (Fig. 5.2f), and algae on sand (Fig. 5.2g). *Halichoeres maculipinna* and *T. bifasciatum* show higher use of *P. porites* rubble than the other species. *Halichoeres bivittatus* shows higher use of sandy microhabitats than the other species. *Halichoeres radiatus* shows higher use of live *P. porites* than the other species.

Study III

The third study method revealed strong differences among life stages (with the addition of TP adult observations) and several differences among the species (Fig. 5.3a - h). The largest ontogenetic differences are found in the following microhabitats: algae on coral rubble (Fig. 5.3a), sand (Fig. 5.3b), and *P. porites* rubble. Juveniles use algae on coral rubble more than IP and TP conspecifics (with the exception of *H. radiatus* and *T. bifasciatum*). Juveniles and IP adults use sand and *P. porites* rubble less than TP conspecifics with a few exceptions among the species.

The largest differences among the species are observed in the following microhabitats:

algae on sand (Fig. 5.3c), *P. porites* rubble (Fig. 5.3d), algae on *A. palmata* (Fig. 5.3e), and *M. annularis* rubble (Fig. 5.3f). *Halichoeres bivittatus* adults and *H. poeyi* juveniles use algae on sand more than conspecifics of different life stages, and the other species. Terminal phase *H. poeyi* and *T. bifasciatum* use *P. porites* rubble more than the other species in a much higher frequency than availability, and *T. bifasciatum* juveniles and IP adults use *P. porites* rubble in higher frequencies than heterospecifics of the same life stage. Initial phase adults of *H. garnoti* and *H. poeyi* use algae on *A. palmata* rubble more than conspecifics of different life stages and heterospecifics. Juvenile *H. garnoti*, *H. radiatus*, and *T. bifasciatum* use *M. annularis* rubble more often than heterospecifics.

Discriminant Function Analysis (DFA): Study I

The groups (life stages and species) were significantly different from each other in multivariate space (Wilk's $\lambda = 0.56$; $F = 6.18$, $df = 80, 5171$; $p < 0.001$ (Table 5.1)). However, there was a poor ability to correctly assign group membership. Only 17% of the fish-occupied quadrats were correctly assigned to the occupant species (i.e. the focal fish). There was a low classification score of 4% of the fish-occupied quadrats correctly assigned to *H. maculipinna* adults, and a high of 53% of the fish-occupied quadrats correctly assigned to *T. bifasciatum* juveniles (Jackknifed classification matrix, not shown). The first discriminant function (DF1) explained 62% of the total dispersion of points (Table 5.1), however, the canonical correlation for DF1 was low, indicating that only 53.7% of the variance is shared between group membership and the microhabitats on each dimension. The microhabitats with the highest canonical scores for DF1 were algae on coral rubble (0.691), and algae on sand (0.694) (Table 5.1, Fig. 5.4). The highest canonical score for DF2 was a strong negative score for *Porites porites* rubble (-0.682) (Table 5.1, Fig. 5.4).

There is a high degree of overlap among the groups (Fig. 5.4). The first discriminant

function (DF1) separates juveniles of the species better than adults. The second discriminant function (DF2) separates adults from juvenile conspecifics. Compared with the other labrids, *Thalassoma bifasciatum* juveniles show lower affinities for algae on coral rubble and algae on sand; whereas *H. bivittatus* and *H. poeyi* juveniles show the highest affinities for these two microhabitats. Along the DF2 axis, adults (with the exception of *H. poeyi*) show lower affinities for *P. porites* rubble than juvenile conspecifics. Null quadrats fall out almost in the center of the discriminant plot, and the farthest group from the null quadrat centroid is *H. bivittatus* juveniles. However, due to the low ability to correctly classify group membership and high overlap in the discriminant plot, no further statistical analyses were conducted to determine if any groups significantly differed from the null quadrats.

DFA: Study II

The statistical results from DFA in study II are similar to those of study I. The groups were significantly different from each other in multivariate space (Wilk's $\lambda = 0.39$; F-statistic = 2.91, $df = 80, 1473$; $p < 0.001$ (Table 5.2). However, there was a poor ability to correctly assign group membership. Only 20% of the focal individuals included in the 5-minute behavioural observations were correctly classified (Jackknifed classification matrix, not shown). The first discriminant function (DF1) explained 50.3% of the total dispersion of points (Table 5.2), however, the canonical correlation for DF1 was low, indicating that only 59.2% of the variance is shared between group membership and the microhabitats on each dimension. The microhabitat with the highest canonical score for DF1 was sand (0.610) (Table 5.2, Fig. 5.5). The highest canonical scores for DF2 were strong positive scores for algae on coral rubble, and live *Montastrea annularis* and *Porites porites* (Table 5.2, Fig. 5.5).

Similar to the discriminant function plot for study I (Fig. 5.4), there is a high degree of overlap among the species and life stages (Fig. 5.5). The first discriminant function separates

Thalassoma bifasciatum juveniles and adults from the other species which suggests that the other species all show an increasing use of sand microhabitats compared with *T. bifasciatum*. Juveniles and IP adults of *Halichoeres poeyi* and *H. bivittatus* have high values of DF1, indicating they show higher affinities for sand microhabitats than the other species.

DFA: Study III

Study III included a small number of TP adults (ranging from 3 to 7 individuals per species), and one recommendation for DFA is that the number of predictor variables used should not exceed the smallest sample size (Tabachnik and Fidell 1989). The results of the discriminant function analyses are included for the data set with and without TP adults included (Tables 5.3 and 5.4, Figs. 5.6 and 5.7). Both analyses showed significant differences among the groups in multivariate space (Wilk's lambda for both data sets were significant at $p < 0.001$ (Tables 5.3 and 5.4). For both data sets, there was a poor ability to correctly assign group membership. When TP adults were included in the data set, only 19% of the total number of fish were classified correctly by percent microhabitat use. Without TP adults, however, the total percentage of fishes correctly classified rose only 7% to 26% (Jackknifed correlation matrices, not shown). The first discriminant function (DF1) with TP adults included explained 61.1% of the total dispersion of points (Table 5.3; 66.8% with TP adults excluded; Table 5.4). The canonical correlations for DF1 for both data sets were higher in this study than study I and study II, indicating that 79.0 % (TP adults included, or 79.2% for TP adults excluded) of the variance is shared between group membership and the microhabitats on each dimension. The microhabitat with the highest canonical score for DF1 from both data sets was sand (0.801 (Table 5.3, Fig. 5.6) or 0.820 (Table 5.4, Fig. 5.7)). The highest canonical score for DF2 when TP adults were included was live *Porites porites* (0.573, Table 5.3). When TP adults were excluded, the highest canonical score for DF2 was a strong positive score for *Porites porites* rubble (0.639, Table 5.4).

Similar to the discriminant function plots for study I and II (Figs. 5.4 and 5.5), there is a high degree of overlap among the species and life stages in Figures 5.6 and 5.7. In both plots, juveniles are separating along the DF1 axis, with *T. bifasciatum* showing the lowest affinity for sand microhabitats, and *H. bivittatus* showing the highest affinity for sand microhabitats. There is a high degree of overlap for *H. maculipinna* and *H. poeyi* juveniles in both plots (Figs. 5.6 and 5.7). The second discriminant function is separating adults from conspecific juveniles, with a high degree of overlap among TP and IP adults. There is a poor ability to separate IP adults into species according to microhabitat use, with the exception of *H. bivittatus*.

Microhabitat availability : proportion of use

The DFA approach to all three studies revealed high degrees of overlap among life stages and species, which may have been caused by high variability among individuals within groups. The approach featured in this section of looking at microhabitat use by individuals in relation to the proportional availability reveals the degree of variability among individuals. These plots (Figs. 5.8 - 5.12) all reveal extremely high variability among the focal fishes. However, there are some interesting trends despite this variability. For example, a large number of *H. bivittatus* juveniles show higher use of algae on coral rubble, algae on sand, and sand than what is available to each individual (open circles fall above the 1:1 use to availability line in Figs. 5.8a, b, and c).

Halichoeres bivittatus IP and TP adults show preference for sand microhabitats, and juveniles and IP adults show avoidance of *Montastrea annularis* rubble. *Halichoeres garnoti* juveniles (Fig. 5.9a - d) show preference for algae on coral rubble, and avoidance of sand and algae on sand. *Halichoeres garnoti* IP and TP adults show preference of sand microhabitats, and IP adults show an avoidance of algae on sand. *Halichoeres maculipinna* juveniles show preferences for algae on coral rubble, and avoidance of sand and algae on sand (Fig. 5.10 a, b, and c). *Halichoeres maculipinna* IP and TP adults show preference for sand, and avoidance of *Montastrea annularis*

rubble. *Halichoeres poeyi* exhibit high variability in use: availability ratios, and the only trends are that many *H. poeyi* of all life stages show avoidance of sand and *M. annularis* rubble, and many *H. poeyi* juveniles also show a preference for algae on coral rubble. *Thalassoma bifasciatum* also exhibits extremely high variability among individuals (Figs 5.12a - d). The only apparent trend is that juveniles and IP adults of this species avoid algae on sand (Fig. 5.12b).

DISCUSSION

Overlap in microhabitat use

Aside from the inconsistencies among the study methods, there were some highly congruent results. For example, after considering all of the analyses, there is a high degree of overlap in microhabitat use in these sympatric labrids. This was not highly surprising, however, these labrids also show high overlap in diet (Randall 1967, Anonymous 1969, Roede 1972, Wainwright 1988) and behaviour (Chapter 4). In a study that compared resource partitioning in fish assemblages in several global habitats (e.g. tropical reefs, temperate reefs, and coastal marine), Ross (1986) found that marine systems show greater importance of trophic separation than habitat separation. He also stated that assemblages from all habitats show rather high separation of coexisting species along at least one resource dimension. The Caribbean labrids in the present study would have created an anomaly in Ross's review.

There is growing evidence that resource partitioning and limiting similarity among coexisting species (Hutchinson 1957, MacArthur and Levins 1967, Abrams 1983) may not be the biblical phenomena driving ecological systems that we once believed. However, it is difficult to disprove untestable hypotheses (Peters 1976). Three typical examples contrary to limiting similarity come from various systems: 1) In freshwater benthic insectivorous fishes, there is growing evidence that biotic interactions may be as great or greater among non-related feeding

guild members as between congeners or species of the same family (Baltz et al. 1982, Resetarits 1995, Taylor 1996). 2) In laboratory experiments with ladybeetles, Evans (1991) found that interspecific competition did not differ significantly from intraspecific competition, in that an individual's weight gain did not depend on whether its competitor was heterospecific or conspecific. 3) In a related system to the present study, Overholtzer and Motta (1999) found that the proportion of microhabitats present within home ranges was similar for all species of juvenile parrotfishes, despite the divergence in resource use and social structure as adults (McAffe and Morgan 1996).

The sympatric labrids in this study coexist with minimal agonistic interactions (Chapter 4), and overlap extensively. It is still difficult to state that interspecific competition is not a primary factor that has affected or continues to affect assemblage structure in this taxonomic assemblage, because it is not known what has occurred historically- in an evolutionary context as well as an ecological context. These species may coexist and show high degrees of overlap now, but exemplify "ghosts of competition past" (Connell 1980). They may have differentiated at a time when resources were limiting, but have now relaxed their divergent traits because resources are no longer in short supply. Multispecies coexistence of ecologically similar species is a complex issue. It can occur because species with sufficiently high dispersal rates persist in sites not occupied by superior competitors (Tilman 1994). It can also occur due to two-way or three-way interspecific trade-offs among competitive ability, colonization ability, and longevity. Coexistence is also a possibility if resources are not in short supply, such is the case in most temperate marine fishes (Barrett 1999), but generalities are uncertain in tropical marine fishes. According to Barrett (1999) for most species of temperate fishes, environmental conditions may influence growth to a greater extent than variations in food availability, plausibly because local population sizes are usually below the level at which competition for food becomes important.

Variability in microhabitat use

There was a very high degree of variability in microhabitat use as shown in the scatterplots of microhabitat availability versus individual use (Figs. 5.8 - 5.12). This demonstrates that labrids are not driven by their surrounding habitats; there may be more important features that affect patterns of labrid distribution and abundance such as landscape patterns (Clarke 1977, Saab 1999) of coral reefs, patterns of recruitment (Caselle and Warner 1996), or biotic interactions (Ebersole 1985, Jones and Syms 1998). Despite the high degree of variability in microhabitat use among individuals, within some life stages and species, a majority of the focal fish consistently selected some microhabitats and avoided others (e.g. many juveniles of most species selected algae on coral rubble; whereas adults selected sand (Figs 5.8 - 5.12); and *H. bivittatus* individuals use sandy microhabitats in greater proportion than availability).

Ontogenetic differences in microhabitat use

In many instances, the results suggested that within some species, ontogenetic differences in microhabitat use were larger than differences among heterospecifics of the same life stage (e.g. Fig. 5.3a - h, and the discriminant function plots (Figs. 5.4 - 5.7)). Some common ontogenetic trends include a decreasing dependence on sheltered microhabitats as they grow (e.g. algae on coral rubble, or algae on *Acropora palmata* rubble), and a corresponding increase in their use of topographically simple microhabitats (e.g. sand or pavement) as they become larger and occupy larger areas. One reason why fishes may reduce their reliance on sheltered microhabitats as they grow is that these microhabitats may become physically inaccessible to adults (Doherty 1983, Shulman 1984, Behrens 1987). In some cases in this study, microhabitats where juveniles were observed would not be suitable to large IP or TP adults, however, it was not always the case.

There are advantages and disadvantages for species that proceed through ontogenetic changes in microhabitat use. Ontogenetic shifts in microhabitat use are present in some species to

alleviate competition between conspecific juveniles and adults (Jones 1980, Jones 1987, Levin 1993, Lirman 1994). There are advantages for juveniles to be attracted to and remain in the same environment as adult conspecifics for “safety in numbers” from predation (Gross and McMillan 1981, Pulliam and Caraco 1984, Magurran 1990), enhanced foraging strategy, and social facilitation or transmission of information (Orians 1961, Helfman and Schultz 1984, Stamps 1987, Shields et al. 1988, and Muller 1998).

Juveniles of some, but not all, marine fish species select habitats that offer cover or increased topographic complexity over open, unprotected spaces (Jones 1984a, b, Carr 1989, DeMartini and Roberts 1990, Holbrook et al. 1990, Levin 1993). For example, Sale (1968) demonstrated that depth preference by juvenile surgeonfish, *Acanthurus triostegus sandvicensis*, depended on the presence of adequate cover. In the absence of cover, smaller juveniles preferred deeper parts of the experimental three-step depth gradient (Sale, 1968). However, there are also examples where habitat cover is not extremely important to juvenile fish. For example, Schmitt and Holbrook (1985) observed that young-of-year preference by a temperate reef fish (the black surfperch, *Embiotoca jacksoni*) for foliose algal patches depended mostly on food quality and secondarily on physical structure, even under high risk from predation. Furthermore, Wennhage and Pihl (1994) studied substratum selection by juvenile plaice (*Plueronectes platessa*) and found that postsettlement stages showed significant preferences for bare sediment compared with areas containing patches of filamentous algae; whereas the later stages appear to prefer the areas containing patches of filamentous algae. Wennhage and Pihl, (1994) suggested that postsettlement larvae may be more cryptic on the bare sandy areas, while adults might prefer areas with more algae for food.

Two species that may be cryptic with certain microhabitats are *Halichoeres bivittatus* and *H. poeyi*. *Halichoeres bivittatus* ranges in colour from white to beige with a lateral line pigmented

black. This species was sometimes observed changing colour to paler white as it swam over sandy microhabitats. All life stages of *H. bivittatus* in this study typically showed stronger affinities for sandy microhabitats than the other species, and in higher proportions than availability.

Halichoeres poeyi is a green labrid that is more commonly found in seagrass habitats than on reefs. However, the corals of Tague Bay became increasingly green with algal turf over the three years of this study (pers. obs.), so *H. poeyi* may benefit from this microhabitat change. Although there were differences across the three study methods, *H. poeyi* juveniles often showed stronger affinities for algal microhabitats than the other species, and in higher frequencies than availability.

Concluding statements

Labrids do not go through obvious ontogenetic shifts in microhabitat compared with grunts, snappers, and grouper that conspicuously shift from seagrass beds to coral reefs when they reach a certain age or size (e.g. Smith and Tyler 1975, McFarland 1979, Brothers and McFarland 1981, Parrish 1987, Eggleston 1995, Sluka and Sullivan 1996)). However, upon closer investigation, ontogenetic differences in microhabitat preferences among conspecific labrids were sometimes greater than heterospecific differences in microhabitat use. As these labrids grow, they decrease their shelter-dependence, and increase their use of topographically simpler microhabitats, perhaps for social or dietary reasons.

These labrid species show high degrees of microhabitat overlap; however, they may have diverged taxonomically at a time when conditions were different than the present (i.e. "ghosts of competition past"). One factor that contributed to the high degree of overlap was the amount of individual variability in microhabitat use. It has often been stated that "when testing for (micro)habitat selection, it is more appropriate to test data for individual animals, rather than pooling data among animals and conducting a single test" (White and Garrott 1990, Manly et al. 1993). It was useful to group the data and average it for general differences. However, it was also

important to look at the variation in microhabitat selectivity among individuals.

Table 5.1. Results of discriminant function analysis predicting species and life stage membership from percent area coverage of eight microhabitat variables in fish quadrats (or null quadrats = without fish). Percent data was angular transformed prior to analysis. Only the first three discriminant functions are presented. Wilk's lambda = 0.56; F -statistic = 6.18 (df = 80, 5171); $p < 0.001$.

Discriminant Function	DF1	DF2	DF3
Canonical Correlation:	53.7	32.1	21.0
Cumulative Proportion of Total Dispersion:	62.1	79.8	86.9
MICROHABITAT	canonical scores:		
algae on coral rubble	0.691	0.354	0.051
<i>Porites porites</i> rubble	0.196	-0.682	-0.114
small rubble	0.294	-0.066	-1.020
<i>Acropora palmata</i> rubble	0.053	-0.044	-0.430
sand	0.472	-0.409	-0.201
algae on sand	0.694	-0.227	-0.192
pavement	0.280	0.233	-0.067
live <i>Porites porites</i>	-0.090	0.350	-0.184

Table 5.2. Results of discriminant function analysis predicting species and life stage membership from percentage of time spent in each microhabitat (eight microhabitats were included in the analysis). Percent data was angular transformed prior to analysis. Only the first three discriminant functions are presented. Wilk's lambda = 0.39; F -statistic = 2.91 (df = 80, 1473); $p < 0.001$.

Discriminant Function	DF1	DF2	DF3
Canonical Correlation:	59.2	44.2	32.8
Cumulative Proportion of Total Dispersion:	50.3	72.8	84.1
MICROHABITAT	canonical scores:		
algae on coral rubble	0.554	0.926	1.216
<i>Porites porites</i> rubble	-0.051	0.782	1.483
<i>Acropora palmata</i> rubble	-0.205	0.893	0.375
sand	0.610	0.468	-0.015
live <i>Montastrea</i> spp.	-0.268	0.953	0.201
live <i>Porites porites</i>	0.085	0.883	0.281
algae on sand	0.444	0.363	0.424
small broken pieces of coral rubble	0.388	0.325	0.683

Table 5.3. Results of discriminant function analysis predicting species and life stage membership from the percentage of observations in each of eight microhabitats (120 observations per focal fish). Terminal phase adults were included in the analysis. Percent data was angular transformed prior to analysis. Only the first three discriminant functions are presented. Wilk's $\lambda = 0.15$; F -statistic = 3.19 (df = 120, 1243); $p < 0.001$.

Discriminant Function	DF1	DF2	DF3
Canonical Correlation:	79.0	55.3	47.1
Cumulative Proportion of Total Dispersion:	61.1	77.4	93.4
MICROHABITAT	canonical scores:		
algae on coral rubble	0.655	0.158	0.180
sand	0.801	0.324	-0.239
algae on sand	0.573	-0.339	-0.198
<i>Porites porites</i> rubble	-0.412	0.383	-0.471
algae on <i>Acropora palmata</i> rubble	-0.176	0.343	-0.230
<i>Montastrea annularis</i> rubble	-0.137	0.040	0.107
pavement	0.432	0.205	0.080
live <i>Montastrea annularis</i>	0.024	0.573	0.649

Table 5.4. Results of discriminant function analysis predicting species and life stage membership from the percentage of observations in each of eight microhabitats (120 observations per focal fish). Terminal phase adults were excluded from the analysis. Percent data was angular transformed prior to analysis. Only the first three discriminant functions are presented. Wilk's $\lambda = 0.18$; F -statistic = 3.88 (df = 80, 985); $p < 0.001$.

Discriminant Function	DF1	DF2	DF3
Canonical Correlation:	79.2	51.7	43.2
Cumulative Proportion of Total Dispersion:	66.8	81.3	90.4
MICROHABITAT	canonical scores:		
algae on coral rubble	0.780	0.300	0.691
sand	0.820	0.317	-0.032
algae on sand	0.690	-0.023	0.096
<i>Porites porites</i> rubble	-0.373	0.639	-0.066
algae on <i>Acropora palmata</i> rubble	-0.056	0.595	0.282
<i>Montastrea annularis</i> rubble	-0.081	0.054	0.192
pavement	0.521	0.354	0.410
live <i>Montastrea annularis</i>	0.150	0.383	0.927

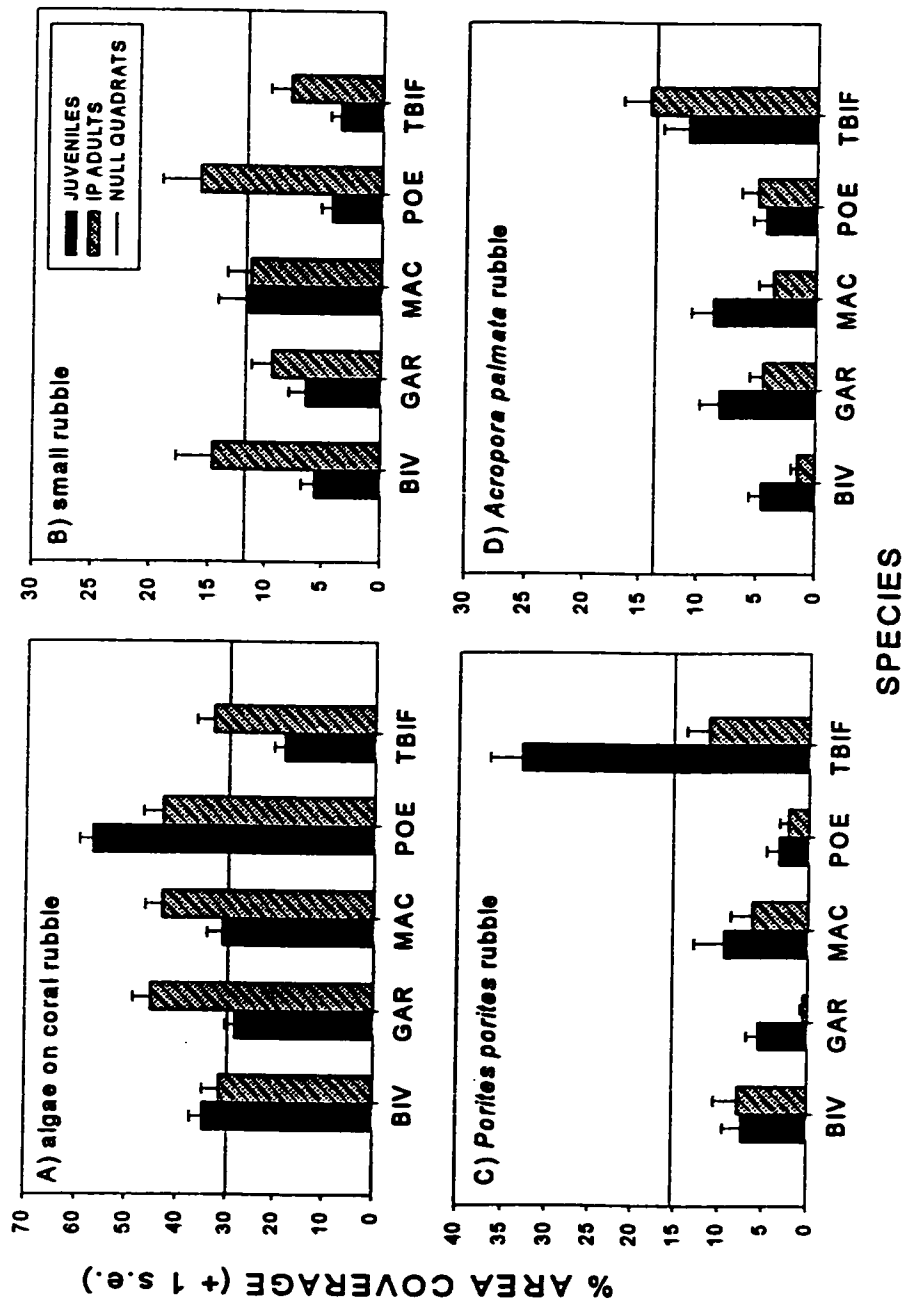


Figure 5.1 a-d. Percent area coverage of the eight most commonly occurring microhabitats in fish-occupied quadrats (1997 data). The following abbreviations are used: BIV = *Halichoeres bivittatus* (n= 62, 55 juveniles and IP adults), GAR= *H. garnoti* (n = 55,52), MAC = *H. maculipinna* (n= 53, 57), POE = *H. poeyi* (n= 55,48), and TBIF= *Thalassoma bifasciatum* (n= 74, 65). The line across each histogram represents the average percent area coverage of the microhabitat depicted in all null quadrats (n= 256).

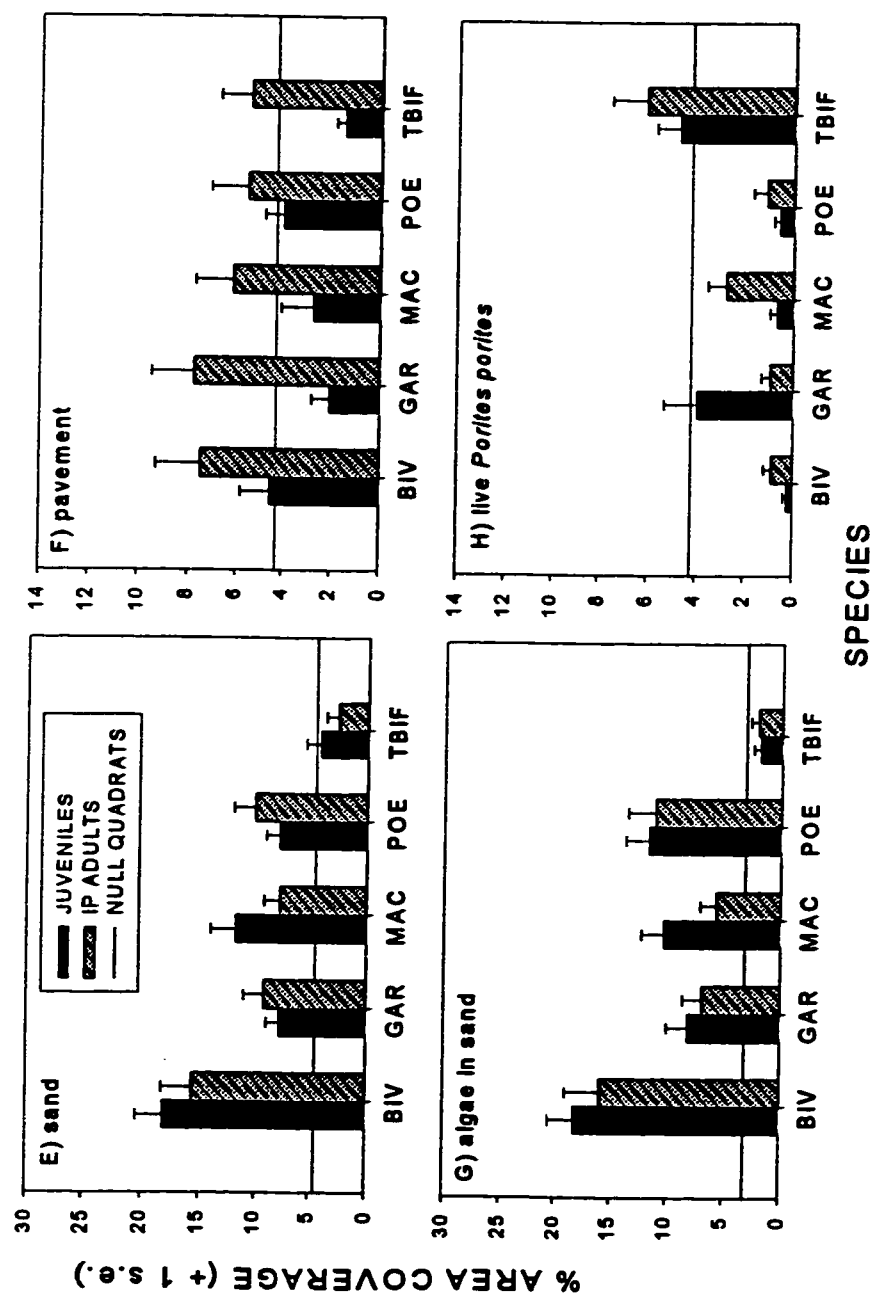


Figure 5.1 e-h. Percent area coverage of the eight most commonly occurring microhabitats in fish-occupied quadrats (1997 data). The following abbreviations are used: BIV = *Halichoeres bivittatus* (n= 62, 55 juveniles and IP adults), GAR= *H. garnoti* (n = 55,52), MAC = *H. maculipinna* (n= 53, 57), POE = *H. poeyi* (n= 55,48), and TBIF= *Thalassoma bifasciatum* (n= 74, 65). The line across each histogram represents the average percent area coverage of the microhabitat depicted in all null quadrats (n= 256).

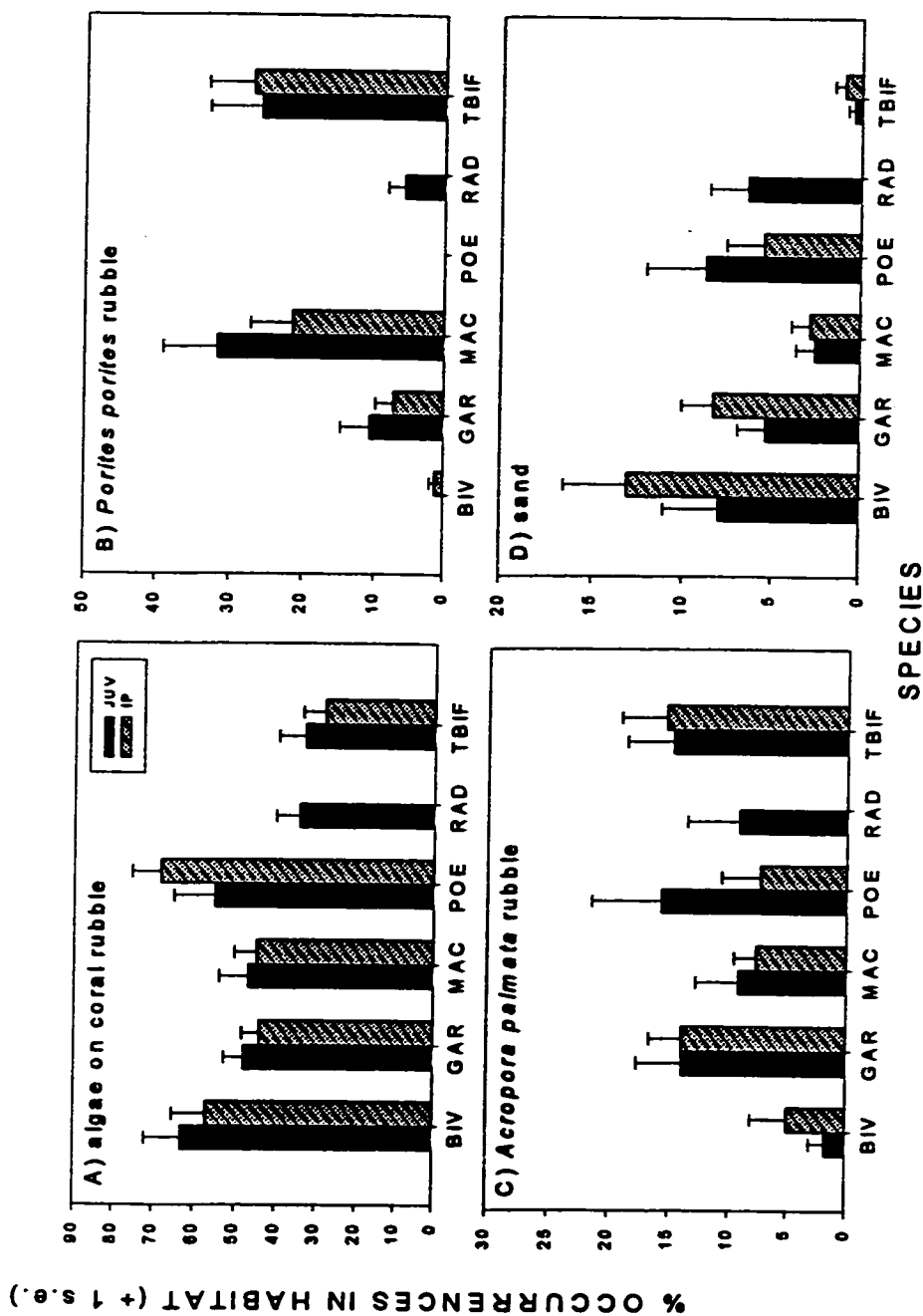


Figure 5.2 a-d. Microhabitat use by juvenile and adult labrids recorded during 5-minute behavioural observations on focal fishes (1997 data). Plotted here are the percent occurrences of labrids in the eight most commonly frequented microhabitats. The same abbreviations are used as in Fig. 5.1, with the addition of RAD = *Halichoeres radiatus*. The sample sizes were as follows: BIV (n= 15, 14 juveniles and IP adults, respectively), GAR (n = 31, 31), MAC (n= 26, 31), POE (n= 11,14), RAD (n = 13 juveniles only), and TBIF (n= 31, 32).

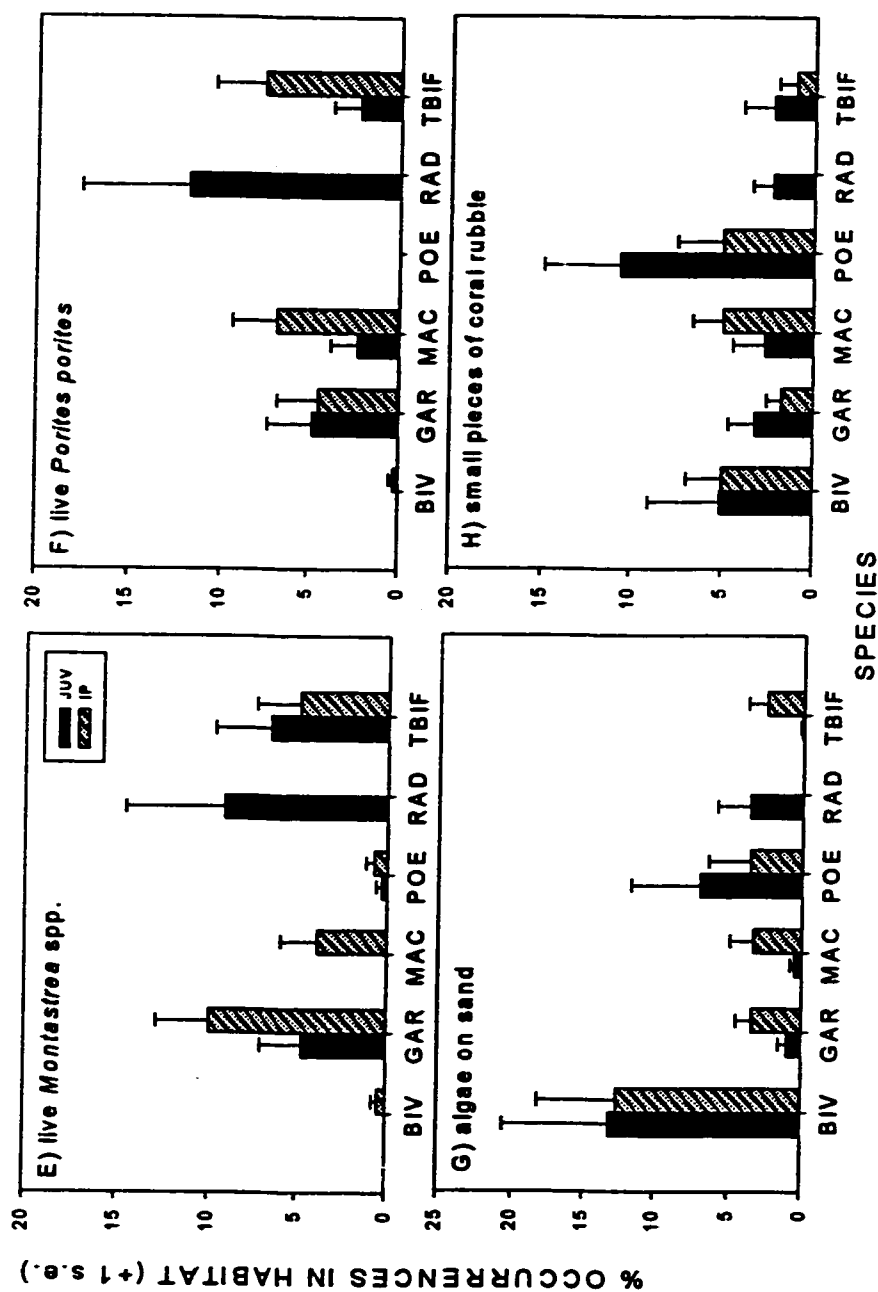


Figure 5.2 e-h. Microhabitat use by juvenile and adult labrids recorded during 5-minute behavioural observations on focal fishes (1997 data). Plotted here are the percent occurrences of labrids in the eight most commonly frequented microhabitats. The same abbreviations are used as in Fig. 5.1, with the addition of RAD = *Halichoeres radiatus*. The sample sizes were as follows: BIV (n= 15, 14 juveniles and IP adults, respectively), GAR (n = 31, 31), MAC (n= 26, 31), POE (n= 11,14), RAD (n = 13 juveniles only), and TBIF (n= 31, 32).

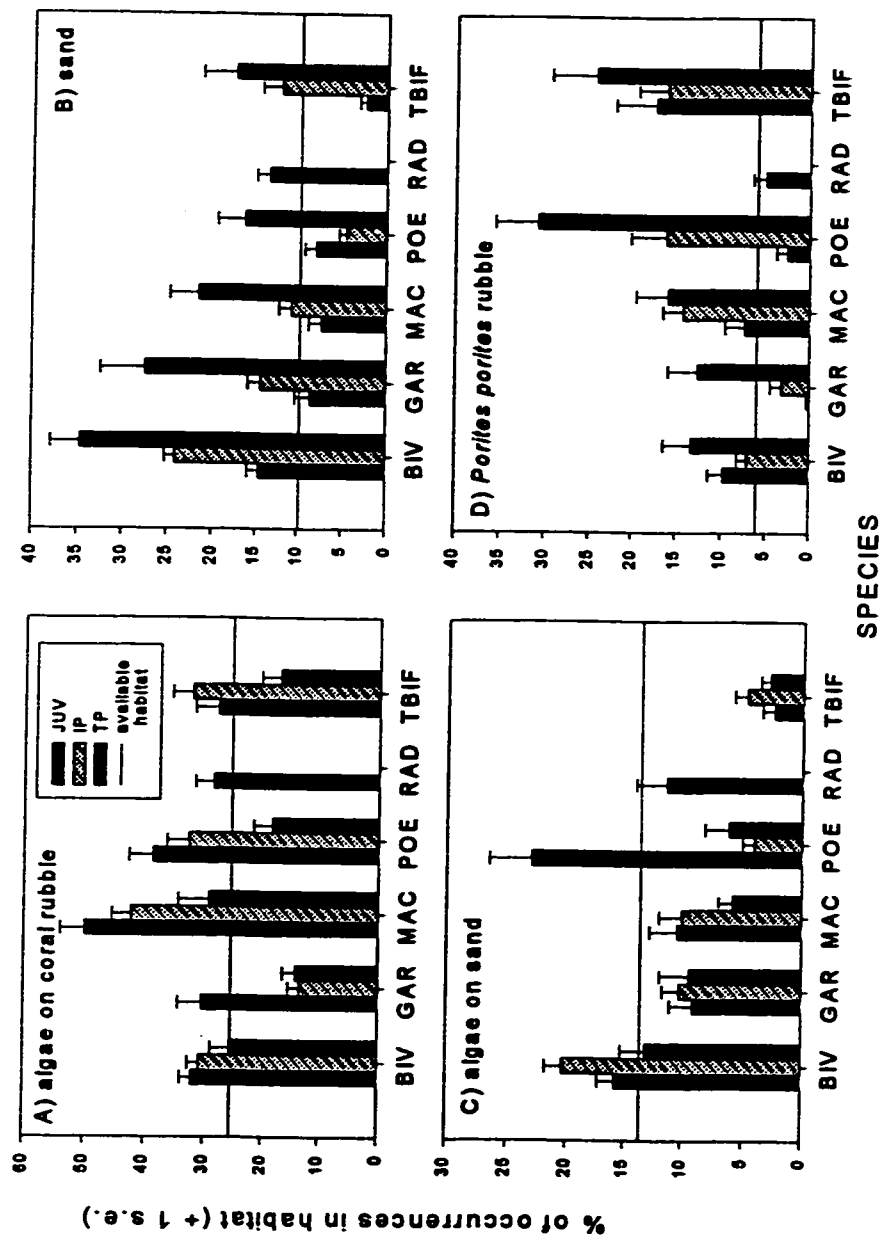


Figure 5.3 a-d. Microhabitat use by juvenile, IP adult, and TP adult labrids recorded during repeated 10-minute observations of microhabitat use within home ranges (1998 and 1999 data). Plotted here are the percent occurrences of labrids in the eight most commonly frequented microhabitats. The same abbreviations are used as in Fig. 5.1 and 5.2. The sample sizes were as follows: BIV ($n = 30, 40$ juveniles and IP adults, respectively), GAR ($n = 11, 11$), MAC ($n = 12, 12$), POE ($n = 12, 11$), RAD ($n = 11$ juveniles only), and TBIF ($n = 11, 11$).

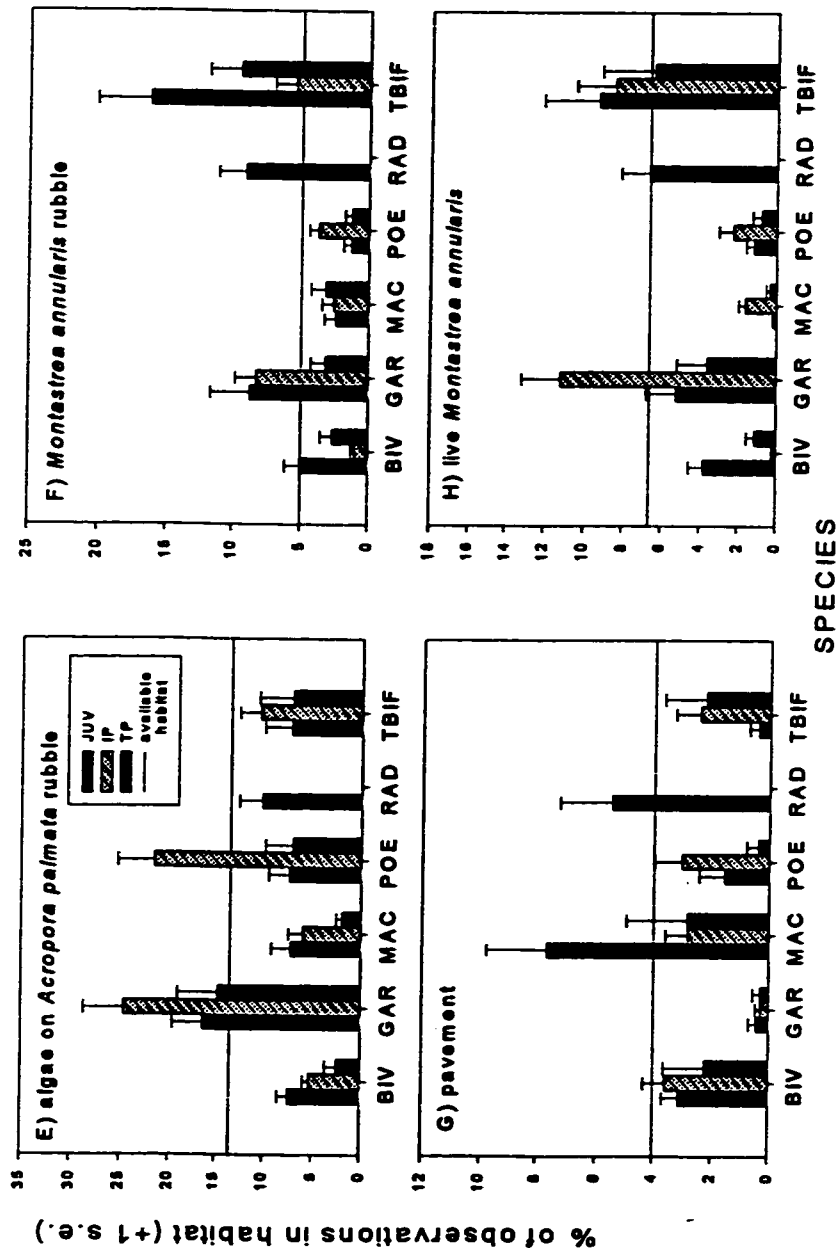


Figure 5.3 e-h. Microhabitat use by juvenile, IP adult, and TP adult labrids recorded during repeated 10- minute observations of microhabitat use within home ranges (1998 and 1999 data). Plotted here are the percent occurrences of labrids in the eight most commonly frequented microhabitats. The same abbreviations are used as in Fig. 5.1 and 5.2. The sample sizes were as follows: BIV (n= 30,40 juveniles and IP adults, respectively), GAR (n = 11,11), MAC (n= 12,12), POE (n= 12,11), RAD (n= 11,11), and TBIF (n= 11,11).

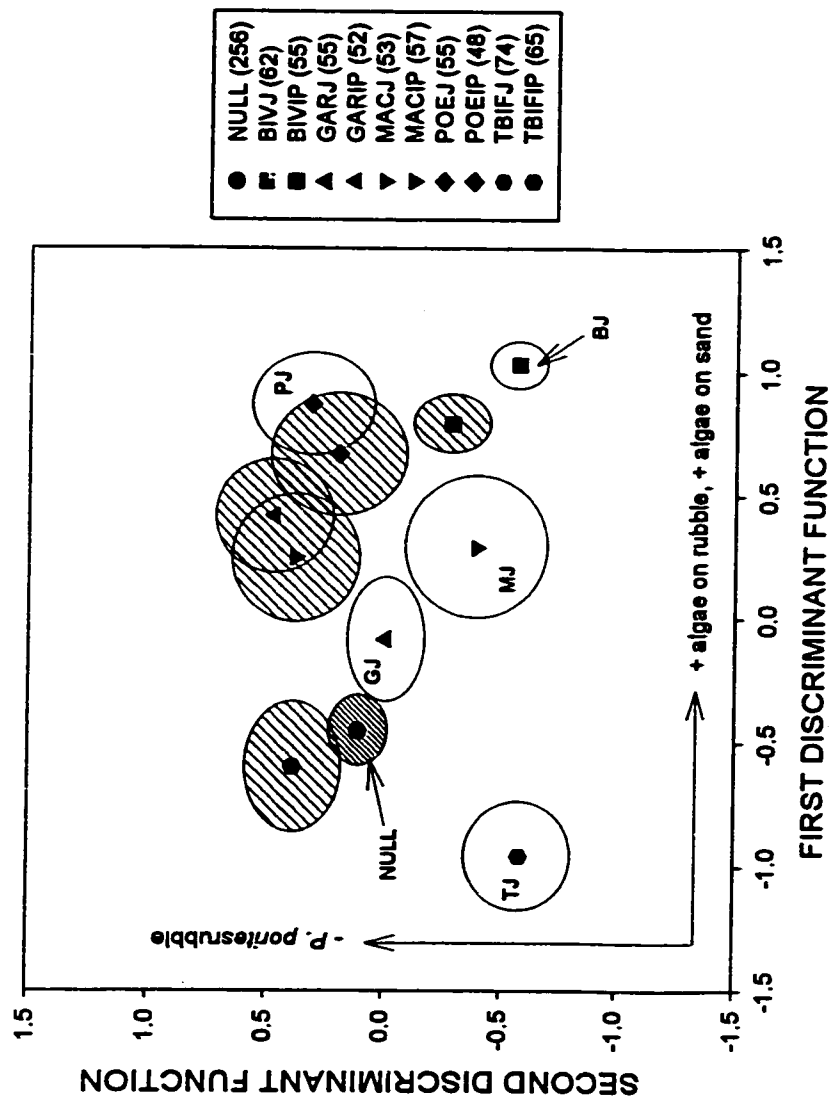


Figure 5.4. Discriminant Function plot of percent area coverage of microhabitats in fish-occupied and null quadrats. The centroids are plotted, and the ellipses encompass the 95% confidence interval of the mean. The open ellipses represent juveniles, and the shaded ellipses (with the exception of the null quadrat ellipse "NULL") represent IP adults. For visual clarity, the juvenile ellipses are also labelled with the first letter of their species name (genus name for *T. bifasciatum*), and the second letter "j" for juveniles. The sample size for the null quadrats and each life stage and species is shown in the legend (the first three letters represent the species name: BIV = *Halichoeres bivittatus*, GAR = *H. garnoti*, MAC = *H. maculipinna*, POE = *H. poeyi*, TBIF = *Thalassoma bifasciatum*; and the last letters represent the life stage: J = juvenile and IP = initial phase adults). Results of the DFA for these data are presented in Table 5.1.

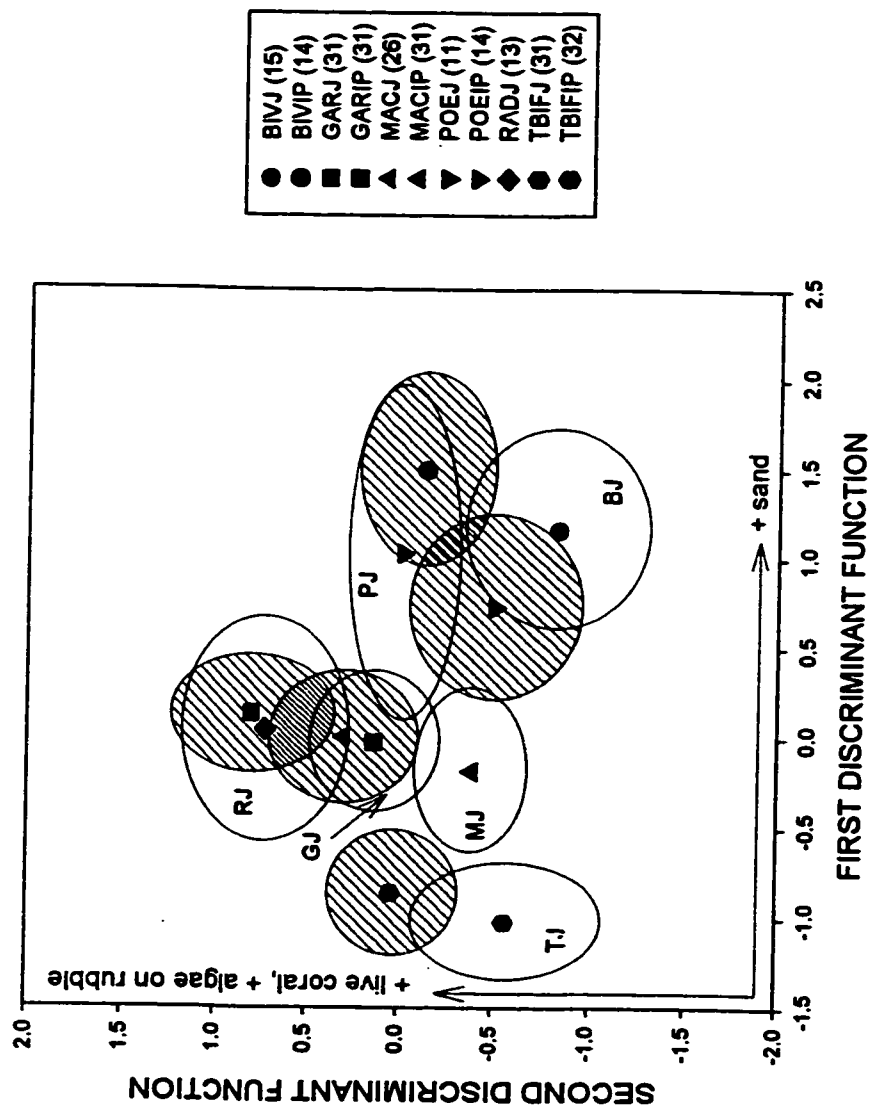


Figure 5.5. Discriminant Function plot of the microhabitat use data collected during 5-minute behavioural observations. The centroids are plotted, and the ellipses encompass the 95% confidence interval of the mean. The sample size for each life stage and species is shown in the legend. The abbreviations for species and life stages are the same as in Fig. 5.2 with the addition of RADJ = *Halichoeres radiatus* juveniles. Results of the DFA for these data are presented in Table 5.2.

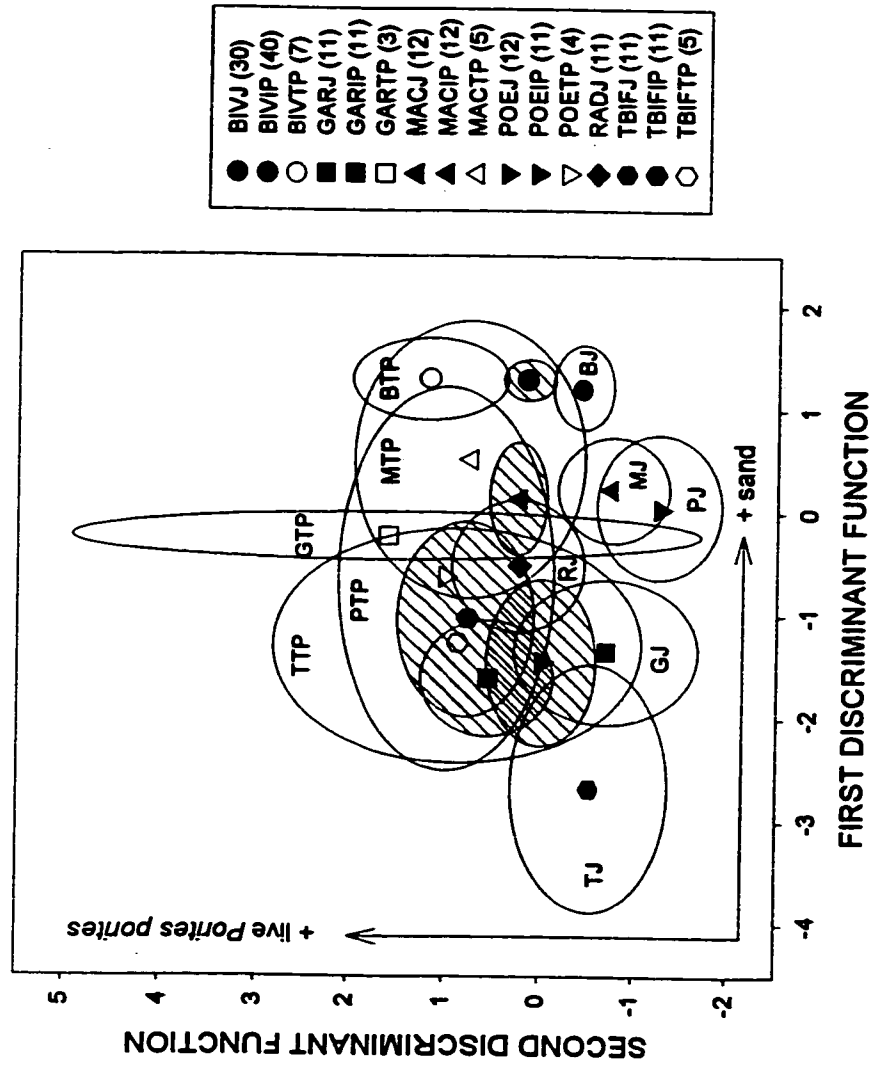


Figure 5.6. Discriminant Function plot of microhabitat use data collected during repeated 10-minute observations on focal fishes within their home ranges. Terminal phase individuals were included in the analysis. The explanation is the same as in Fig. 5.4 and 5.5. Results of the DFA for these data are presented in Table 5.3.

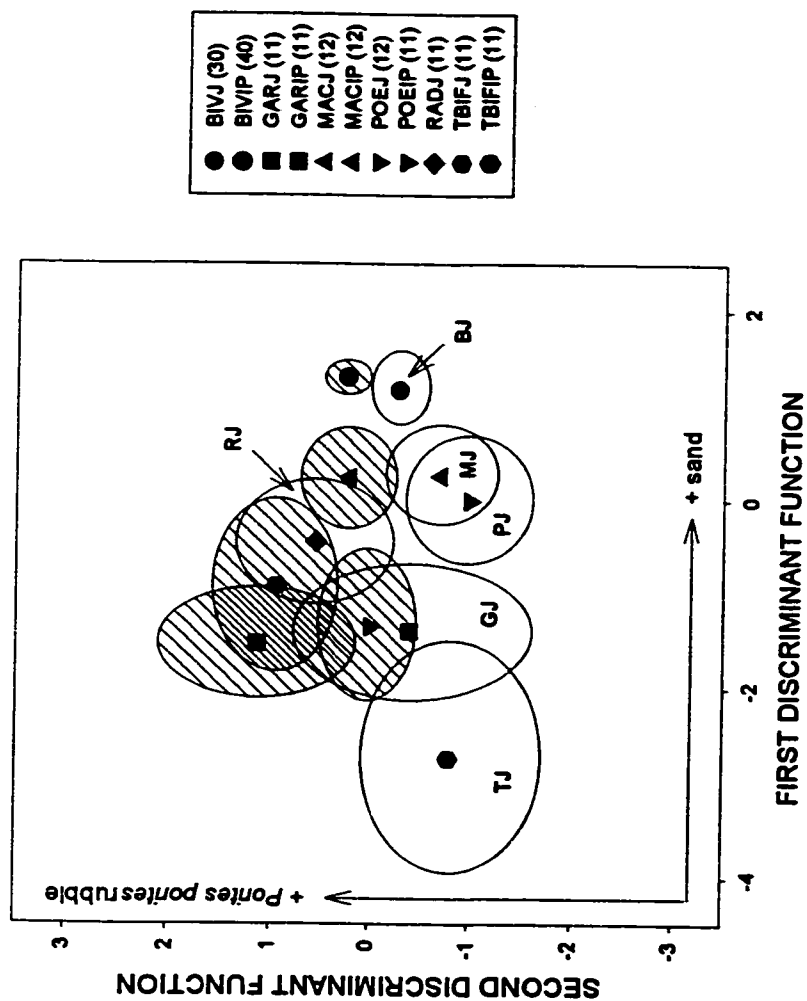


Figure 5.7. Discriminant Function plot of microhabitat use data collected during repeated 10-minute observations on focal fishes within their home ranges. Terminal phase individuals were excluded from the analysis. The explanation is the same as in Fig. 5.4 and 5.5. Results of the DFA for these data are presented in Table 5.4.

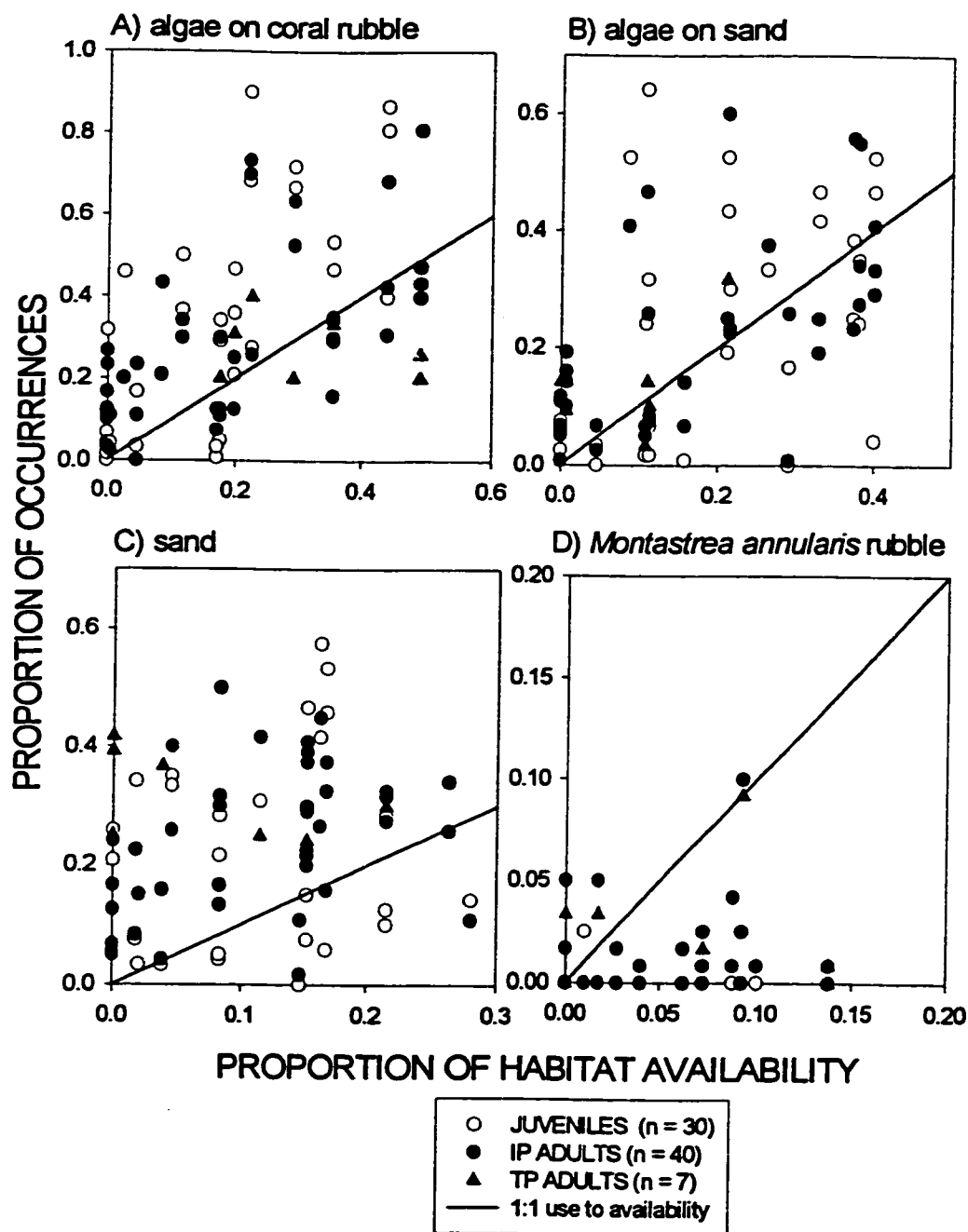


Figure 5.8 a-d. Microhabitat availability versus proportion of use in *Halichoeres bivittatus*. The line represents where the individuals would fall if they used microhabitat solely on an availability basis. The proportion of microhabitat availability was calculated from microhabitat quantification within the 10x10m quadrat within which the individual's home range was located.

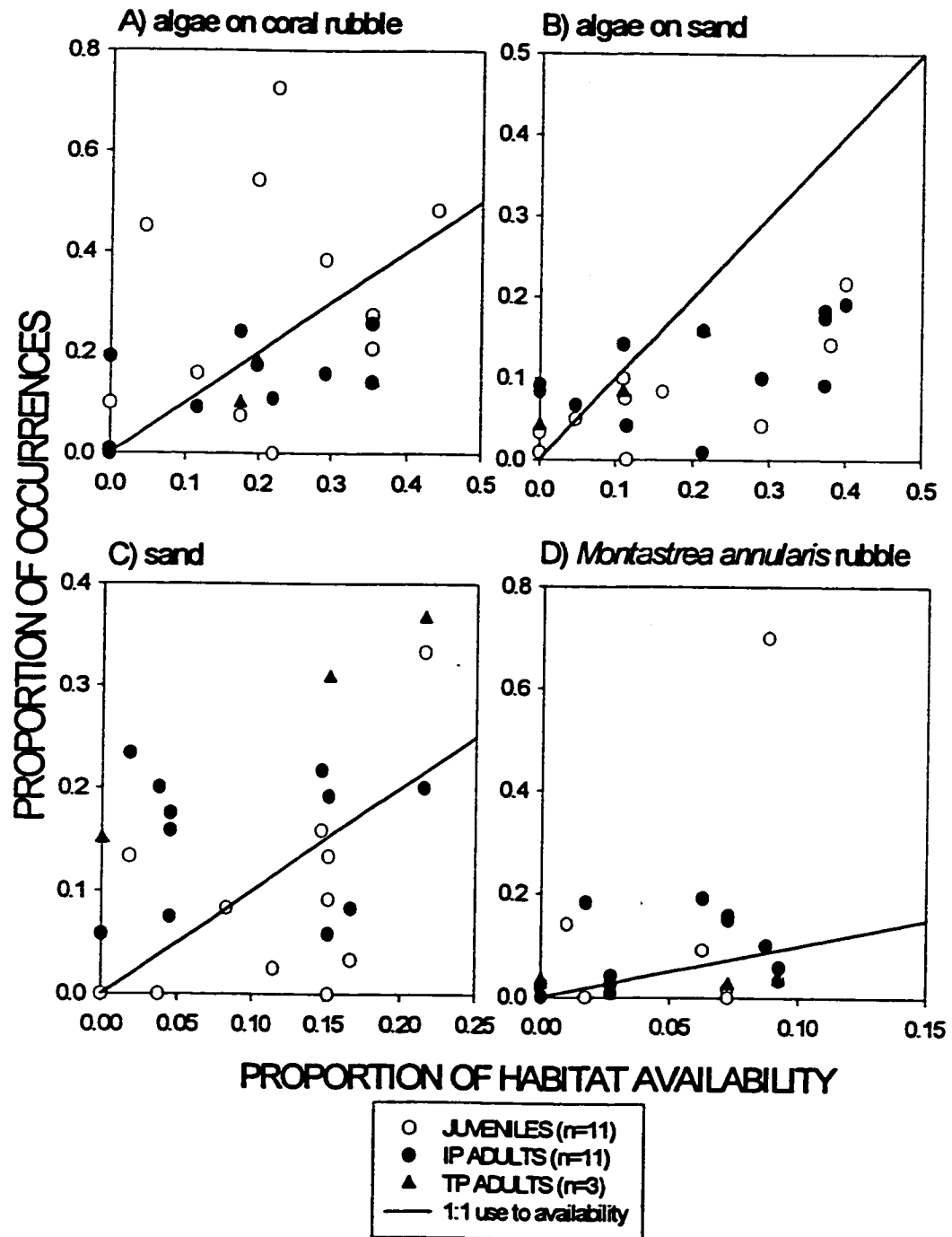


Figure 5.9 a-d. Microhabitat availability: proportion of use in *H. garnoti*. The explanation is the same as in Fig. 5.8.

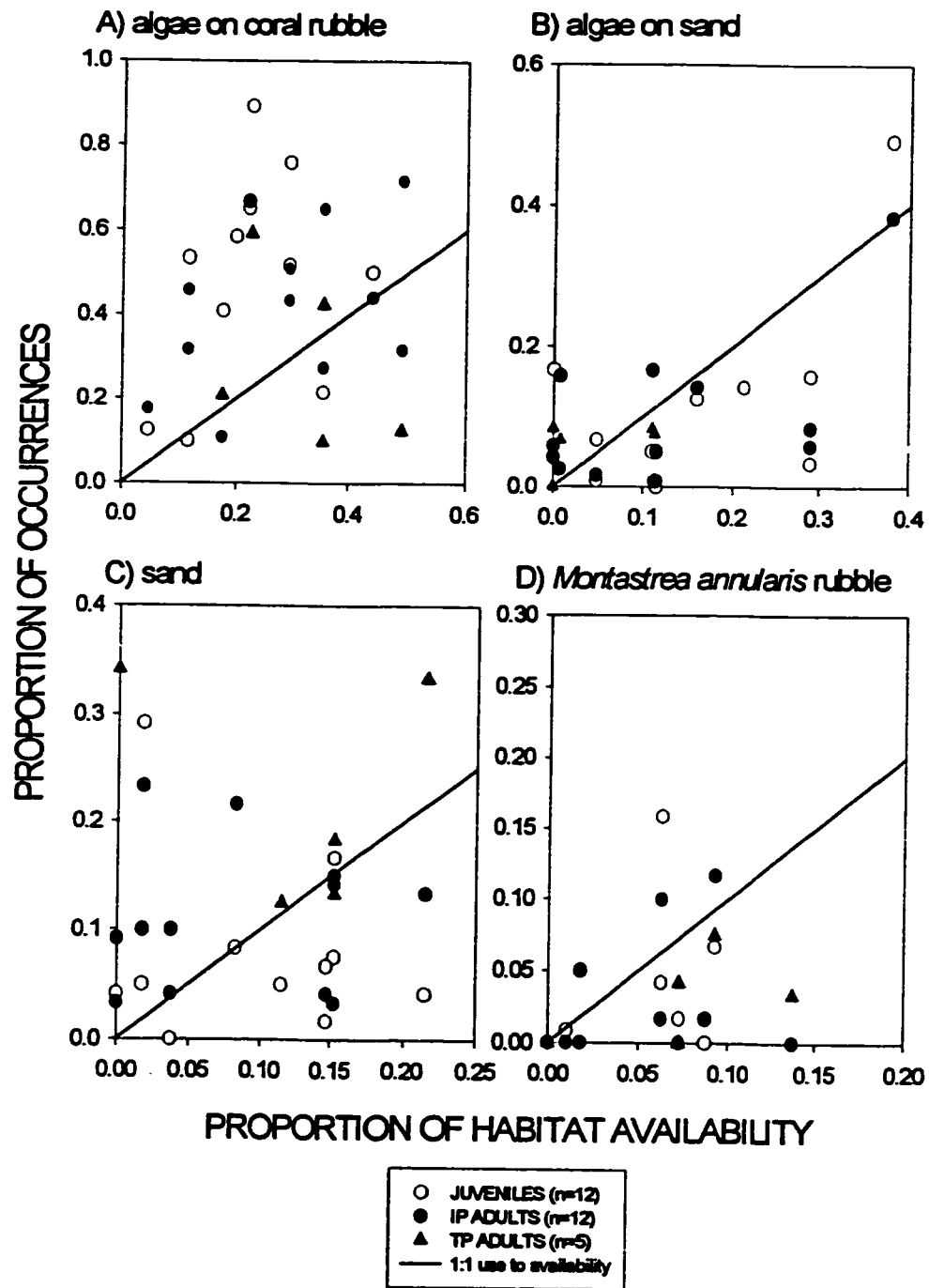


Figure 5.10 a-d. Microhabitat availability: proportion of use in *H. maculipinna*. The explanation is the same as in Fig. 5.8.

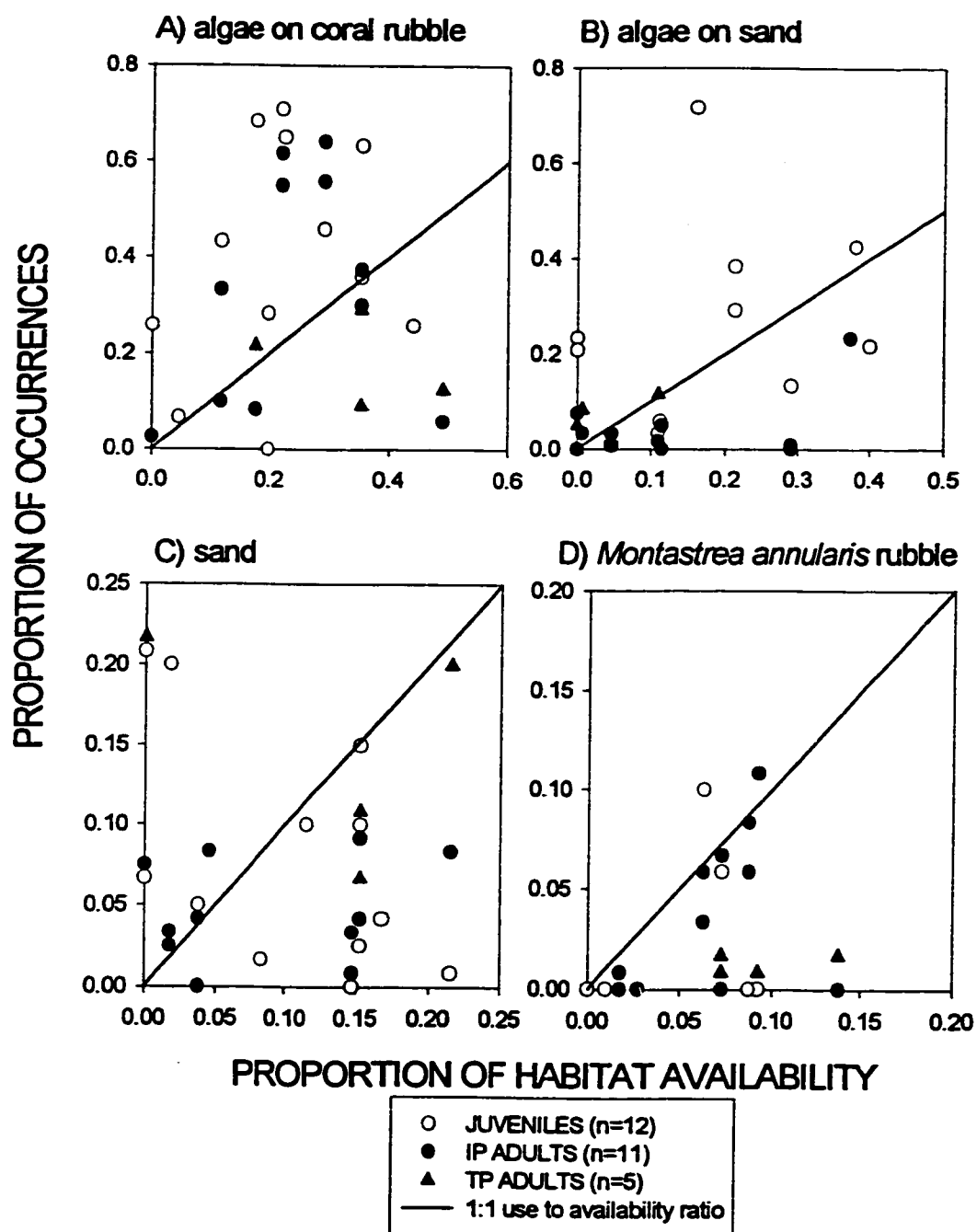


Figure 5.11 a-d. Microhabitat availability: poportion of use in *H. poeyi*. The explanation is the same as in Fig. 5.8.

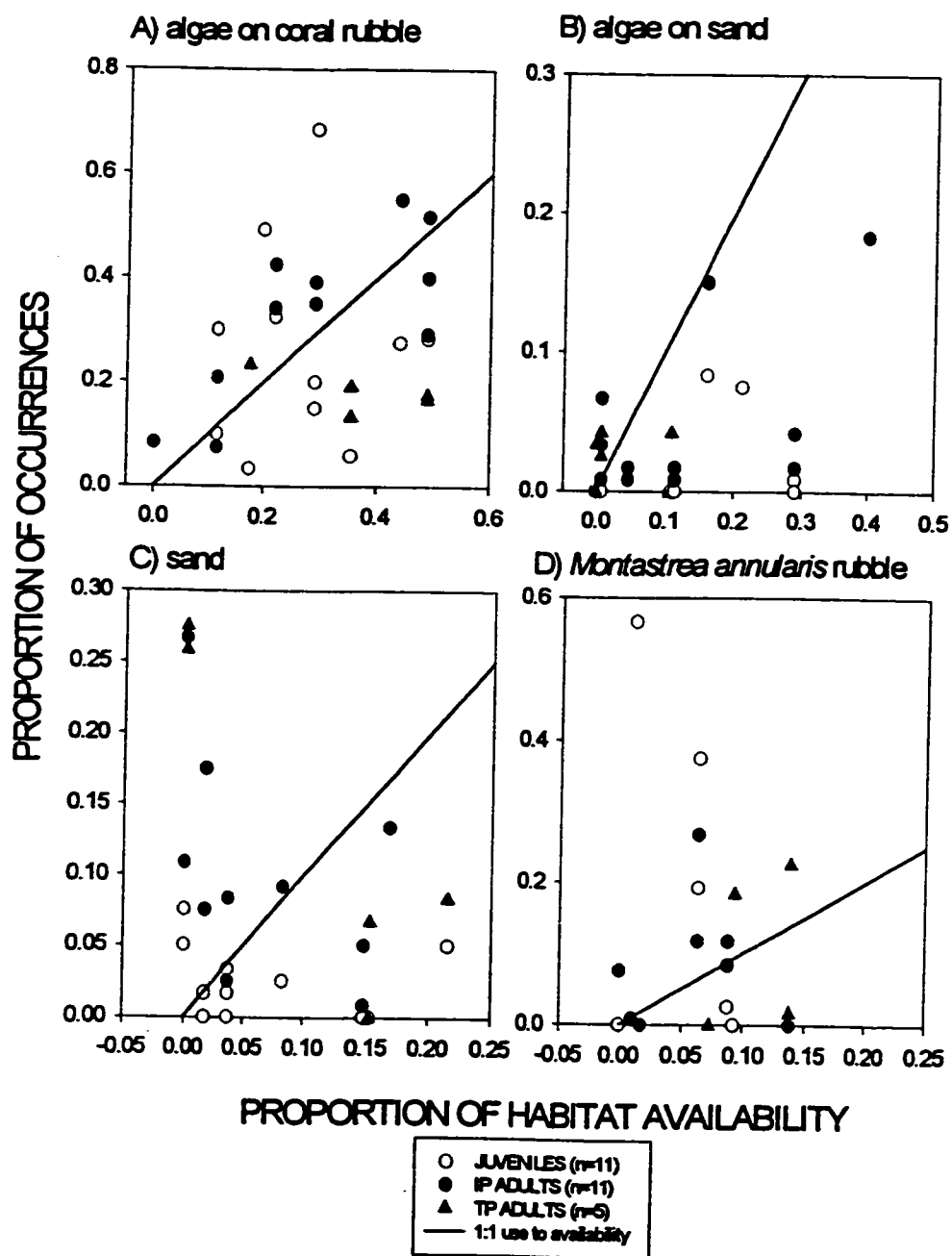


Figure 5.12 a-d. Microhabitat availability: proportion of use in *Thalassoma bifasciatum*. The explanation is the same as in Fig. 5.8.

CHAPTER VI

**THE EFFECT OF TERRITORIAL POMACENTRIDS ON THE SPATIAL
DISTRIBUTION AND BEHAVIOURAL DYNAMICS
OF THE CARIBBEAN LABRID, *HALICHOERES BIVITTATUS***

ABSTRACT

Most demersal species of damselfish (Family Pomacentridae) are territorial herbivores that aggressively chase other fishes, including wrasses (Family Labridae) away from their nests. This study investigated the effect of beaugregory damselfish, *Stegastes leucostictus*, on the behaviour and home range parameters of the slippery dick wrasse, *Halichoeres bivittatus*. A manipulative field experiment consisted of transplanting one or three beaugregories into artificial shelters positioned within adult or adjacent to juvenile slippery dick home ranges. Home range areas prior to the manipulations averaged $4.3 \pm 0.3\text{m}^2$ for juveniles, and $31.6 \pm 1.6\text{m}^2$ for adults. The total length of slippery dicks explained 91% of the variation in home range area. Introduction of beaugregory damselfish appeared to have no effect on home range area for either juveniles or adults, although they had a significant effect on the location of home ranges by causing slippery dicks to move away from introduced beaugregories. There was also a significant effect on microhabitat use in adults, but not juveniles. In addition, there was a significant increase in beaugregory-slippery dick interactions. This resulted in a significant reduction in the amount of time adult slippery dicks could spend foraging or in a foraging assemblage. Overall, results of this experiment suggest that aggressive interactions with territorial pomacentrids affect individual space

use in the slippery dick wrasse. These interactions may consequently affect the spatial distribution of slippery dick populations. The aggressive interactions between damselfish and slippery dicks may lead to fitness consequences for individuals by reducing foraging time and modifying the behavioural interactions between adult slippery dicks and their foraging assemblages.

INTRODUCTION

The spatial distribution of animal populations and space use by individuals have long been central issues in ecology. Animals are usually not randomly distributed in space, instead they orient with respect to surrounding animate and inanimate objects (Martin and Salvador 1995). Individual space use can ultimately determine the spatial distribution and dynamics of populations and communities (Fryxell and Lundberg 1998). The number of individuals in populations and communities that can live together in a given space depends on the amount of microhabitat available, the size of the home range required by each individual, and the extent to which the space can be shared by other individuals of the same or different species (Smith and Tyler 1972). There are several factors that affect space use by individuals, including: availability of habitat or microhabitat (Smith and Tyler 1972; Jones 1984a; Ebersole 1985; Stamps and Buechner 1985; Gerking 1994; Martin and Salvador 1995; Robertson 1996; Baras 1997; Marvin 1998; Aparicio and de Sostoa 1999), food resources (de Jong 1979; Gerking 1994; Rolando 1998), presence of predators (Mittelbach 1986; Coleman and Wilson 1996; Auster et al. 1997; Gregory and Anderson 1997; Werner et al. 1983), and presence of competitors (Smith and Tyler 1972; Stamps and Buechner 1985; Robertson 1996).

Studies involving space use by animals have revealed that individuals of many species from various taxa have home ranges. A home range is typically defined as the area in which an individual performs its daily activity cycle (Burt 1943; Gerking 1994; Barrows 1996). Territories

are simply home ranges which are actively defended (Gerking 1994). Because animals occasionally make exploratory excursions outside these areas of normal activity (Anderson 1982; Thibault and Bovet 1999), the home range is commonly specified as an area within which some fixed percent of activity falls (most often 95%)(Anderson 1982; Worton 1989). Although many kinds of home range occupation (e.g. active defense) can exist, there is a continuum of the spacing systems across animals (Maher and Lott 1995). Three discrete systems can represent the gradient: dominance usually refers to a priority system (or hierarchy) based on overt or subtle aggression; despotism is a specialized form of dominance in which one animal, the despot, is dominant to the others that are all of equal rank; and finally, a “no defense” system, in which animals group together with no spatial relationships other than perhaps individual space (Maher and Lott 1995). The coral reef fish used in this study, *Halichoeres bivittatus*, has a harem mating system that affords dominance to a terminal phase male. However, outside of the spawning period, minimal agonistic encounters were observed (*pers. obs.*). This implies a spatial system somewhere between despotism and “no defense”.

Several studies on many fish species have examined the effect of habitat, species interactions, and other environmental factors on spatial positioning or home range parameters, for example: catfish, *Barbus barbus* (Baras 1997), pumpkinseed sunfish, *Lepomis gibbosus* (Coleman and Wilson 1996); pikeperch, *Stizostedion lucioperca* (Jepsen et al. 1999); yellowfin shiner, *Notropis lutipinnis* (Goforth and Foltz 1998); the black piranha, *Serrasalmus rhombeus* (Cohen et al. 1999); and blacksmiths, *Chromis punctipinnis* (Bray et al. 1981). There has also been a general trend reported for long-term site attachment in many coral reef fishes (Sale 1971; Robertson and Hoffman 1977; Barrett 1995; Holland et al. 1993; Kramer and Chapman 1999); including several reef fishes of Families Labridae and Monacanthidae (Barrett 1995), Serranidae (Shapiro 1987), red snapper, *Lutjanus campechanus* (Szedlmayer and Shipp 1994), the coral

trout, *Plectropomus leopardus*, (Zeller 1997), the humbug damselfish, *Dascyllus aruanus* (Sale 1971), and white goatfish, *Mulloidides flavolineatus*, (Holland et al. 1993). The sedentary nature of reef fishes is not unexpected because familiarity with a section of the reef offers the advantage of intimate knowledge of feeding, sleeping, mating, and shelter sites, and the location of potential competitors (Reinboth 1973; Wootton 1990; Barrett 1995; Braithwaite 1998; Kramer and Chapman 1999). Kramer and Chapman (1999) have reviewed the implications of home range size and relocation in the establishment of marine reserves for coral reef fishes. Additional knowledge of factors that may affect home range parameters and relocation will benefit marine reserve managers.

Many factors can influence the area, shape, and location of an animal's home range (Melville and Swain 1999). In many different taxa, there appears to be a direct relationship between home range area and size of individual (McNab 1963; Sale 1978a; Fitch and Shapiro 1990; Gerking 1994; Minns 1995; Eifler 1996; Kramer and Chapman 1999), although there are many exceptions to this relationship (e.g. Ebersole 1980; Aparicio and de Sostoa 1999; Melville and Swain 1999). In studies where direct allometric relationships have been found between home range size and size of individual, there is no clear consensus about the reasons why this relationship exists. It is becoming increasingly clear that home range area is not simply determined by the interaction of food resources and energetic requirements alone; instead, habitat availability and social factors (e.g. location of mates or potential competitors) may also influence home range area (Melville and Swain 1999). In many studies, it has been found that home ranges are irregular in shape (Fitch and Shapiro 1990) and although some of these irregularities are explained by habitat structure, many are not. This study investigates the effect of social interactions, by means of interspecific competition, on both the area and shape of home range use in the Caribbean labrid, *Halichoeres bivittatus*.

In terrestrial ecology, there has been a recent recognition that territories and home ranges are not fixed parcels of real estate (Eifler 1996; for a review see Gordon 1997). Instead, home range boundaries are continually adjusting as a result of behavioural interactions or physical disturbances in the surrounding environment. Investigating the effect of behavioural interactions can be intrinsically difficult because the intensity of interactions among individuals depends on their spatial positioning, and the interactions themselves modify these spatial positions (Slatkin and Anderson 1984). Few studies have investigated the effect of behavioural interactions on spatial dynamics (but see Jones 1984a; Itzkowitz 1977b; Coleman and Wilson 1996). One study by Jones (1984a) suggested that aggressive interactions and interspecific foraging associations influenced the behaviour and use of space by the temperate labrid, *Pseudolabrus celidotus*. However, he inferred that these activities probably only had a transitory influence on the spatial distribution of this wrasse. Itzkowitz (1977b) observed that uni-specific adult colonies of Caribbean pomacentrids were a result partly due to a behavioural system which inhibits other species from sharing a common territorial border on a homogeneous substratum. An additional goal of this study was to investigate experimentally the fluid mosaic of home range use and shifting individual boundaries in coral reef fish communities.

Communities of reef fishes provide excellent opportunities to investigate behaviours and space use. Many fishes are found in close proximity to one another, and direct visual observations and manipulative field experiments are relatively easy compared with other ecological systems. The two species that were chosen to address the hypothesis that aggressive interactions with territorial individuals can modify space use in the less aggressive, non-territorial species were the beaugregory damselfish, *Stegastes leucostictus*, which is a territorial pomacentrid (Family Pomacentridae), and the slippery dick wrasse, *Halichoeres bivittatus* (Family Labridae), a wider ranging forager.

Many labrids are exceedingly abundant where they occur, especially smaller species such as two Caribbean species: the bluehead, *Thalassoma bifasciatum*, and the slippery dick, *Halichoeres bivittatus* (Bohlke and Chaplin 1968; Roede 1972). Their ubiquitous distributions and interesting characteristics (e.g. protogynous hermaphroditism and spawning behaviours) make them favorable study organisms for coral reef ecologists. They are carnivorous and often voracious feeders, and *H. bivittatus* are commonly seen in foraging assemblages with conspecifics, heterospecific labrids, and juvenile members of the surgeonfish, butterflyfish, and parrotfish families (Acanthuridae, Chaetodontidae, and Scaridae, respectively) (*pers. obs.*). Juvenile *H. bivittatus* are more commonly solitary or with conspecific juveniles and swim close to the substrate, but as they grow larger and their home range area increases, they swim higher above the substrate in larger foraging assemblages (*pers. obs.*). Minimal aggressive interactions were observed among *H. bivittatus* and other members of their foraging assemblages unless high quality food items were located (such as crustaceans or molluscs). Overall, very few agonistic interactions were recorded, according to the descriptions of aggressive behaviour for related labrids, the cunner, *Tautoglabrus adspersus* (Pottle and Green 1979), and the bluehead wrasse, *Thalassoma bifasciatum* (Fitch and Shapiro 1990). These authors listed such behaviours as approach, chase, lateral display, parallel swimming, frontal display, and biting as aggressive behaviours. *H. bivittatus* are microhabitat generalists (Chapter V), but their home range area must encompass at least some form of structural relief for protection, as well as a minimal area of sand. Many labrids dig themselves into sandy bottoms to sleep at night (Reinboth 1973), or as a last resort to quickly evade predation (*pers. obs.*). Agonistic interactions between labrids and pomacentrids are commonly observed where members of these families co-occur.

Pomacentrids are known to be very aggressive towards conspecifics or heterospecifics entering their territories (Sale 1971; Clarke 1977; Itzkowitz 1977a,b; Thresher 1984; Ebersole

1985; Allen 1991; Santiago and Castro 1997). The strongest attacks are directed at potential egg predators, including many labrid species (Reinboth 1973; Katzir 1981; Ferreira et al. 1998). Egg predators have the greatest relative impact on the reproductive success of the damselfish. Myrberg and Thresher (1974) found that a related species, *Stegastes planifrons* defends different sized territories against individuals of different species. In many pomacentrids, it has been demonstrated that individuals are capable of discriminating between species; subsequently, their level of aggression towards different species that invade their territories can be modified accordingly (Myrberg and Thresher 1974; Katzir 1981; Ferreira et al. 1998). Beaugregory damselfish, *Stegastes leucostictus*, can apparently distinguish among approximately fifty different species of reef fishes that invade their territories (Ebersole 1977). Male damselfish territories encompass food (algae), a spawning site, the eggs spawned there, refuge holes that provide both protection from predators and a place where the territory holder can rest at night. In general, *S. leucostictus* is a microhabitat generalist because it has been shown to use all types of coral heads (Ebersole 1985), and is estimated to have a very localized territory of approximately 2-4m² (*per. obs.*). Territory areas have been calculated for closely related damselfish species: *Stegastes dorsopunicans*- 2.10 +/- 0.36m² (Ferreira et al. 1998), *S. dienaecus*- 3.1m²; *S. partitus*- 4.5m²; *S. planifrons*- 2.5m² (Luckhurst and Luckhurst 1978).

The main objective of this study was to determine the effects of the presence of territorial pomacentrids, *Stegastes leucostictus*, on the home range parameters, spatial dynamics, and behavioural interactions of the Caribbean labrid, *Halichoeres bivittatus*. Subsequently, this study addresses whether or not *H. bivittatus* show fluid, or plastic responses in their home range boundaries after *S. leucostictus* are introduced into the center of adult home ranges, or adjacent to juvenile home ranges. It was hypothesized that damselfish introductions compared to control treatments would cause the focal individual *H. bivittatus* to: 1) reduce their home range area, 2)

relocate their home range position, or show low percentage overlap with original home range location, 3) use alternative microhabitats, 4) increase the amount of time spent interacting with damselfish, which would subsequently decrease the amount of time spent foraging or in foraging assemblages, and 5) swim higher above the substrate in order to avoid encounters with the introduced damselfish.

MATERIALS AND METHODS

Study species

The focal animal for this study was the slippery dick wrasse, *Halichoeres bivittatus*. Juvenile *H. bivittatus* used in this experiment averaged 3.5 ± 0.1 cm (mean \pm 1 s.e.; $n = 24$) in total length (TL), and adults averaged 12.0 ± 0.2 cm (TL; $n = 24$). An additional 29 individual *H. bivittatus* were observed for home range area in a preliminary study (Chapter II), and their home ranges and total lengths were pooled with the experimental individuals to investigate the relationship between size of fish and home range size. Individuals used in the experiment were distinguished by size and colour characteristics or abnormalities in the lateral line. This method of identifying individuals proved to be effective in a preliminary study that compared the use of tags and natural characteristics.

The territorial pomacentrid used in this study was the beaugregory damselfish, *Stegastes leucostictus*. Only adult males of this species were used because the male of a spawning pair is responsible for guarding the demersal eggs from egg predators like *Halichoeres bivittatus*. Individuals used in this experiment were between 6-8 cm in fork length.

Site Description

All observations were carried out on the back reef zone (or lagoonal area) along the continuous reef tract of Tague Bay, northeast St. Croix, U.S.V.I. The study quadrats were located

in depths of 2–4 m, so direct visual observations were made by snorkeling. Algae growing on coral rubble (algal turf) was the predominant substratum, followed by dead *Porites porites*, dead *Acropora palmata*, other small, broken pieces of dead coral, and sand. Other live corals such as *Siderastrea* spp., *Diploria* spp., and *Agaricia* spp., as well as gorgonians, sponges, and seagrass beds occurred but were less common in the study areas. This study was carried out from May to August 1999.

Maps and Observations of Home Range Use and Behaviours

The microhabitats in twelve quadrats ($10 \times 10 \text{ m}^2$) were mapped on sheets of acetate, and mylar was placed on top of each map to record observations of the focal individuals (grid size represented 0.25 m^2). Two adults and two juveniles of *H. bivittatus* were observed in each quadrat, with no overlap in the adult home ranges. The juveniles selected for observation were close to the core use area of the focal adult. Experimental treatments were randomly assigned.

Home range parameters and behaviours of juvenile and adult *H. bivittatus* were determined prior to the experimental manipulations. Four repeated observation periods of 10 minutes were conducted on each individual *H. bivittatus*. During each observation period, the following data were recorded every 20 seconds on a map: position of the focal individual (which was translated into Cartesian coordinates), microhabitat use, behaviour, with whom the focal individual was interacting, and swimming distance above the substrate. The observation periods were done on separate days, and the order of individual fish observations was randomized on each day. Additional observations were not found to significantly affect either the estimation of home range area or the behavioural time budgets.

Experimental Manipulation

Two treatment densities of pomacentrids and two controls were used (Fig. 6.1). The two pomacentrid treatments were the introductions of either one or three *Stegastes leucostictus*. This

was accomplished by placing terracotta roofing tiles (Fig. 6.1) into the home range of the focal adult *H. bivittatus* individual, and adjacent to the home range of the focal juvenile *H. bivittatus*. Male *S. leucostictus* were caught with a drop net under terracotta tiles placed in locations away from the experimental quadrats and were then transplanted into the experimental tiles. After damselfish were transplanted into the tiles, they were observed for 15 minutes to determine whether they were going to take up residence in the tile. For those damselfish that swam away after translocation, the process of catching and translocating individuals was repeated until one damselfish remained in the tile and actively defended it after transplantation (only two damselfish during this process swam away and had to be replaced). The manipulation was left for 48 hours prior to observing the effects of the introduction of tiles (the controls) or damselfish and tiles on adult and juvenile *H. bivittatus*. After the manipulation, the same observations were recorded as before.

Home Range Area

Home range areas were calculated through the use of CALHOME (Kie et al. 1994; default value of 0 was used for estimating optimum bandwidth). The adaptive kernel method (AK) (Worton 1989) was used to calculate home range area because the number of points observed per individual was relatively high (120 per animal, compared to mark and capture techniques that have fewer sampling points and use minimum convex polygon calculations instead). The adaptive kernel method has a smoothing parameter (or bandwidth) that calculates the probable areas of movement based on the distribution of points (Worton 1989). All home range areas reported for this experiment represent the 95% utilization distribution, which defines the area in which an individual *H. bivittatus* spends 95% of its typical activity cycle.

To determine if home range areas were consistently smaller after damselfish introductions, the following ratio was calculated for each *H. bivittatus*, and then averaged within control and

treatment groups:

$$\frac{\text{home range area after the manipulation (m}^2\text{)}}{\text{home range area before (m}^2\text{)}} \times 100 \quad (\text{Equation 1})$$

Assumptions of normality and homogeneity of variances were met (all statistical analyses for this study were performed with SigmaStat). One-way ANOVAs were performed on juveniles and adults separately with ratio of area before versus after as the yield variable, and treatment group as the main factor.

Home Range Relocation (% Overlap)

To determine if damselfish introductions cause *H. bivitattus* to relocate their home range areas, the plots of home ranges from CALHOME were digitized into the program MOCHA (1993), and home range areas before and after the manipulation were overlaid. The percentage overlap in home range relocation was determined by the following equation:

$$\frac{\text{overlap area (m}^2\text{)}}{\{(\text{area before (m}^2\text{)} + \text{area after (m}^2\text{)}) / 2\}} \times 100 \quad (\text{Equation 2})$$

Percentage overlap was angular transformed to meet assumptions of normality and homogeneity of variances. Data were analyzed through a one-way ANOVA with arcsin square root{% overlap} as the yield variable and treatment group as the main factor. Juveniles and adults were analyzed separately.

Microhabitat use

Additional to home range coordinates, microhabitat use within the experimental quadrats was also recorded. The main microhabitat categories included: dead *Acropora palmata*, live *Porites porites*, dead *Porites porites*, live *Montastrea annularis*, dead *Montastrea annularis*, algae growing on coral rubble, algae or seagrass fronds surrounded by sand, unidentifiable coral

rubble, *Porites astreoides*, *Agaricia* spp., *Millepora complanata*, *Siderastrea siderea*, *Diploria* spp., other live coral species, gorgonians, sea fans, pavement (hardened, planar surfaces of coral sometimes covered in a thin layer of sand), sponges, sand, and seagrass (most commonly *Thalassia testudinum*). To see if beaugregory introductions cause *H. bivittatus* to use alternative microhabitats, a comparison of microhabitat use before versus after the manipulations was analyzed. Because size and arrangement of microhabitat types determines the microhabitats available to an animal (Wilson et al. 1998), it is more appropriate to test for microhabitat selection within individual animals, rather than pooling data among animals and conducting a single test (Manly et al. 1993). Czekanoswki's proportional similarity index (Feinsinger et al. 1981, Sale and Guy 1992) was used to compare microhabitat use within individuals before versus after the manipulation:

$$C_{ij} = 1 - \frac{1}{2} \sum_{k=1}^s |p_{ik} - p_{jk}| \quad (\text{Equation 3})$$

Variables p_{ik} and p_{jk} are the proportion of time before and after the manipulation, respectively, spent in the k^{th} microhabitat. There are s microhabitat categories. An individual fish with a maximal value of 1.0 for C_{ij} indicates that the percentage of time spent in each of the microhabitat categories before versus after the manipulation was identical. The smaller the value, the greater the deviation from the original distribution of time spent in each microhabitat. The values calculated with Czekanowski's Index were angular transformed to meet assumptions of normality and homogeneity of variances. The data were analyzed for juveniles and adults separately through one-way ANOVAs with arcsin square root {Czekanowski's Index} as the yield variable, and treatment group as the main factor.

Behavioural Time Budgets

Along with observations of microhabitat use, behaviours were simultaneously recorded. Behaviours observed during preliminary investigations with labrids (Jones *in prep.*) that were found to contribute substantially to labrid time budgets included: eating/biting = actively biting at the surface, touching substrate with nose, swimming alone, swimming with only conspecifics, swimming with only heterospecifics, swimming with both conspecifics and heterospecifics, being chased, chasing another fish (when one fish attempted to bite or swam rapidly at another fish that swam away, the interaction was called a chase (as per Shulman 1985; Fitch and Shapiro 1990; and Itzkowitz 1990)), looking at the substrate, eye flickering, hovering with the tail curled (C-shape), hiding, opening mouth while maintaining a hovering position, “bobbing” or moving up and down in the water column (head first, then tail), and touching or rubbing body on the substrate.

For statistical analyses, behavioural categories were reduced to six based on incidence and means, and a seventh category that combined all behaviours that could be defined as “foraging behaviours”. Juvenile behaviours included: eating, hovering, damselfish chases, bobbing, touching nose to substrate, swimming alone, and “foraging” = eating + touching nose to substrate. Adult behaviours included: swimming with conspecifics and heterospecifics (which combined swimming with only con- or only heterospecifics and swimming with both con- and heterospecifics), swimming alone, touching nose to substrate, chased by damselfish, hovering, bobbing, eating, and “foraging” = swimming with conspecifics and heterospecifics + touching nose to substrate + eating. To determine if beaugregory introductions have a significant effect on the amount of time *H. bivittatus* spends doing different activities, one-way ANOVAs were used to analyze the effects on juvenile and adult behaviours separately. The yield variable for the analysis was the following ratio:

$$\frac{\% \text{ of time spent doing the behaviour after the manipulation}}{\% \text{ of time spent doing the behaviour before}} \times 100 \quad (\text{Equation 4})$$

No transformations were made prior to analyses because assumptions of equal variance and normality were met.

Social interactions

While recording behaviours of focal individuals, I also recorded with whom they were doing these behaviours. Social interactions occurred with juvenile and adult conspecifics, heterospecific labrids, and fishes from other families (predominantly pomacentrids, scarids, and acanthurids). A social interaction was loosely defined as an interaction with any fish less than two body lengths away from the focal fish (as per Breder 1959), and apparently engaged in the same activity (e.g. biting surface, swimming). The focal fish was solitary if the closest fish was greater than two fish lengths away from the focal individual. However, a pomacentrid interaction was an exception to these definitions. A pomacentrid interaction was recorded when a damselfish actively chased a focal *H. bivittatus*, or reacted to it in an aggressive manner (e.g. pectoral flares, darting towards the focal individual, or a tail flick which was often accompanied by a clicking noise). These interactions often occurred when the focal individual and the pomacentrid were greater than two body lengths apart.

The hypotheses tested were that beaugregory introductions would cause an increase in the social interactions between *H. bivittatus* and the introduced beaugregories, which would subsequently cause a reduction in the social interactions with other fishes. To test these hypotheses, one-way ANOVAs were carried out for juvenile and adult *H. bivittatus* separately, on each of the social interactions recorded. The social interactions recorded were reduced to seven for statistical analyses based on means and incidence, and an eighth category, “foraging assemblage”,

combined social interactions with members of typical foraging groups (conspecific adults and juveniles + heterospecific juvenile and adult labrids + juvenile acanthurids and scarids). The seven social interactions of importance to juvenile *H. bivittatus* included those with conspecific juveniles, conspecific adults, scarid juveniles, *Stegastes leucostictus* juveniles and adults combined, *S. leucostictus* adults alone, and *S. leucostictus* juveniles alone. The seven social interactions of importance to adult *H. bivittatus* included those with conspecific adults, conspecific juveniles, scarid juveniles, acanthurid juveniles, *Stegastes leucostictus* adults alone, and *S. leucostictus* juveniles and adults combined. The yield variable for each ANOVA was the following ratio:

$$\frac{\% \text{ of time spent interacting after the manipulation}}{\% \text{ of time spent interacting before}} \times 100 \quad (\text{Equation 5})$$

and the main factor was the treatment group. The data were not transformed prior to analysis because assumptions of normality and homogeneity of variances were met.

Swimming distance above the substrate

While observing focal fish, their swimming distance above the substrate was estimated. Estimations were placed in five categories because it was difficult to quantify the exact height above the substrate. The distance categories above the substrate included: I) touching the surface, II) 1-2 cm III) 3-5 cm, IV) 6-10cm, and V) 11-50 cm. To determine if beaugregory introductions caused *H. bivittatus* to alter their patterns of swimming distance above the substrate (which may have exposed them to greater predation risk), t-tests on means were used to test for differences in the percentage of time spent in each of the distance categories before versus after the experimental manipulation.

RESULTS

Relationship of home range area to size of fish

Home range area showed a significant direct and positive log-log relationship with size of *H. bivittatus* (Fig. 6.2). Size of fish (TL in cm) explained 90.8% of the variation in home range area (95% AK in m²) ($p < 0.001$). Home range areas (95 % AK) of the experimental individuals prior to the manipulations averaged $4.3 \pm 0.3\text{m}^2$ for juveniles, and $31.6 \pm 1.6\text{m}^2$ for adults. Juvenile *H. bivittatus* used in this experiment averaged $3.5 \pm 0.1\text{cm}$ (mean \pm 1 s.e.; $n = 24$) in total length (TL), and adults averaged $12.0 \pm 0.2\text{cm}$ (TL; $n = 24$).

Effects of damselfish introductions on home range area

Analysis of the ratio of home range area after the manipulation versus before revealed no significant differences between control and treatment groups for either juvenile or adult *H. bivittatus* (One-way ANOVA for juveniles: $F = 1.931$, $p = 0.157$; One-way ANOVA for adults: $F = 0.216$, $p = 0.888$)(Fig. 6.3). A value of 120% would indicate that the home range area after the manipulation was on average 20% larger than before. The controls (empty shelters) and treatments (beaugregory introductions) all affected the home range areas of both juvenile and adult *H. bivittatus*. However, there were no consistencies in effect, demonstrated by the high degree of standard error in Fig. 6.3. There appears to be a slight trend in juveniles for smaller home range areas after beaugregory introductions compared with controls, but it was not statistically significant.

Effects of damselfish introductions on home range relocation (% Overlap)

Juvenile *H. bivittatus* were forced to reposition their home range location when beaugregories were introduced adjacent to the original home range area (One-way ANOVA: $F = 10.422$; $p < 0.001$)(Fig. 4). Their new home range locations overlapped by approximately 20% with their original home range areas in the two treatment groups, compared with approximately 55

and 65% overlap for the two controls (Tukey's *post hoc* tests where $p < 0.05$: 1 D < 1 T, 1 D < 3 T; 3 D < 1 T, 3 D < 3 T, as shown by lines in Fig. 6.4). Adult *H. bivittatus* were forced to relocate substantially only in the treatment group with three beaugregories introduced into the core of the home range area (One-way ANOVA: $F = 5.597$; $p = 0.006$, Fig. 6.4). Adult home ranges in this treatment group overlapped only 45 % with their original home range area, compared to 60-65% overlap in the two control groups and the treatment with only one beaugregory introduction (Tukey's *post hoc* tests where $p < 0.05$: 3 D < 1 T; 3 D < 3 T, as shown by lines in Fig. 6.4).

Effects of damselfish introductions on microhabitat use

Czekanowski's proportional similarity index revealed that juveniles in control and treatment groups all showed low similarities in the distribution of time allocation in each of the microhabitat categories before versus after the manipulation (Fig. 6.5). Differences in microhabitat configurations across individuals within the same control or treatment group has been controlled by using Czekanowski's Index. For juveniles, there were no significant differences with respect to shifts in microhabitat use after the experimental manipulations among control and treatment groups (One-way ANOVA: $F = 2.816$; $p = 0.065$). In contrast, adult *H. bivittatus* altered the distribution of time allocation in each of the microhabitat categories in each of the two treatment groups (One-way ANOVA: $F = 17.627$; $p < 0.001$)(Fig. 6.5) compared with the controls. Czekanowski's proportional similarity index revealed only 0.50-0.60 congruence in the distribution of time allocation in each of the microhabitats for the two treatment groups compared with 0.78-0.85 for the two controls (Tukey's *post hoc* where $p < 0.05$: 1 D < 1 T, 1 D < 3 T; 3 D < 1 T, 3 D < 3 T).

Effects of damselfish introductions on behavioural time budgets

Juvenile and adult *H. bivittatus* spend different amounts of time performing various behaviours (Table 6.1). The eight most common behaviours for juveniles and adults are listed in

Table 6.1, along with the average percentage of time spent doing those behaviours. For example, two apparent differences between juveniles and adults are that juveniles spend a significant amount of time “flickering their eyes” (almost 20% of their time), which is predominantly a juvenile behaviour; whereas a significant behaviour for adults is swimming alone (20% of an adult’s time is spent swimming alone, compared with only 8% for juveniles). Eye flickering is simply when the focal fish hovers in the water column while performing very pronounced eye twitches or rotations of the eye. This is thought to be a behaviour that promotes alertness or awareness of potential predators. In general, juveniles were more sedentary than adults, stayed closer to the substrate, and spent a greater amount of time solitary or with other juvenile conspecifics. Swimming in larger, mixed foraging assemblages was more common for adults than juveniles, thus social interactions with conspecifics, heterospecific labrids, acanthurids and scarids were considered to contribute to “foraging” behaviours for adults but not juveniles (“foraging” for juveniles was comprised of eating + touching nose to the substrate).

Experimentally, I wanted to determine if damselfish introductions resulted in increased numbers of chases between *H. bivittatus* and the introduced beaugregories, which would subsequently cause a reduction in the amount of time the focal individuals spent in other important activities. Results of One-way ANOVAs that tested for differences between the controls and treatment groups are presented in Table 6.2, and differences in the percentage change in some important behaviours are presented in Fig. 6.6.

For juveniles, the only behaviour that was significantly affected by the introduction of damselfish was the amount of time spent being chased by damselfish (Table 6.2). Juveniles in the treatment group with three beaugregories introduced, more than doubled the amount of time spent chased by damselfish (approximately 245%, Fig. 6.6A). However, this increase in % time spent chased by damselfish did not result in any significant reductions for any other juvenile behaviours,

including “foraging” (Table 6.2, and Fig. 6.6B). Eye flickers were reduced after beaugregory introductions, but the differences were not statistically significant ($p = 0.059$, Table 6.2).

In contrast, for adult *H. bivittatus*, damselfish introductions resulted in a significant increase in the % time spent chased by damselfish, which subsequently caused a reduction in the % time spent “foraging” (Table 6.2, Fig. 6.6 C and D). The treatment group with three beaugregories caused a doubling in the amount of time adults spent in agonistic interactions with damselfish (200%, Fig. 6.6C). This doubling converts 7% of their activity time devoted to encounters with damselfish, to approximately 14% for those *H. bivittatus* in closer proximity to higher numbers of beaugregories (extrapolated from Table 6.1, and Figure 6.6C). Likewise, with three beaugregories added, there was a loss of approximately 15% of the amount of time adult *H. bivittatus* could spend “foraging” (Fig. 6.6D). This loss of 15 % converts the average amount of time spent “foraging” from 41% to approximately 35% of the time budget (Table 6.1). A loss of 6% of foraging time in a time budget could have substantial effects over a longer term.

Effects of damselfish introductions on social interactions

Some of the results for social interactions were similar to those results observed for changes in behaviour. The amounts of time spent interacting with conspecifics, scarids, acanthurids, and pomacentrids are presented in Table 6.3. The amount of time spent in a foraging assemblage was calculated by combining the social interactions with members of typical foraging groups (conspecific adults + juveniles + heterospecific juvenile and adult labrids + juvenile acanthurids and scarids). There was no significant effect of the experimental manipulations on the amount of time spent in a foraging assemblage for juveniles (Results of the one-way ANOVAs, Table 6.4). The only result that was significantly different in juvenile *H. bivittatus* was the increase in amount of time spent in an agonistic interaction with beaugregories when three beaugregories were experimentally introduced (Table 6.4, Fig. 6.7A). For adult *H. bivittatus*, there was also a

significant effect due to the beaugregory introductions (Table 6.4, Fig. 6.7B). Both levels of beaugregory introductions resulted in a significant increase in beaugregory- *H. bivittatus* interactions for adult *H. bivittatus* (Fig. 6.7B). This significant increase in agonistic social interactions with beaugregories resulted in a decrease in the amount of time adult *H. bivittatus* spent interacting with scarid and acanthurid juveniles, and with the foraging assemblage (Table 6.4, Fig. 6.7 C and D). Interestingly, the introduction of either one or three empty shelters (the controls) resulted in a 50% increase in the amount of time adult *H. bivittatus* spent interacting with scarids after the manipulation (Fig. 6.7C) which suggests some artifactual benefit of providing tiles, or an enhancement of these social interactions. A significant reduction in the amount of time adults spent in a foraging assemblage could adversely affect them not only by reducing foraging time, but also by decreasing the other advantages of being in a group.

Effects of damselfish introductions on swimming distance above the substrate

Only results for the treatment with three damselfish introduced are presented (Fig. 6.8) because the results for all the controls and treatment groups were extremely similar. It is apparent from the histograms presented that juveniles spend a greater amount of time closer to the substrate (categories I - IV, or lower than 11 cm off the substrate), and adults spend a greater amount of time higher above the substrate (category V, or higher than 11 cm). It is also apparent that within a size class, there was a great deal of rigidity or consistency in the amount of time individuals spent in each of the distance categories (apparent through the very small error bars for $n = 6$). This suggests that there is minimal plasticity in this behaviour, both within and among individuals. There were no significant differences before versus after for any distance categories in any of the controls or treatments ($p > 0.05$ for all t-tests).

DISCUSSION

This study investigated the effects of a territorial pomacentrid on the behaviours, social interactions, and spatial dynamics in a wider ranging forager, *Halichoeres bivittatus*. The results suggest that the pomacentrid, *Stegastes leucostictus*, has substantial effects on individual *H. bivittatus* that may translate into effects on a population level. Although *S. leucostictus* did not significantly affect home range area for either juvenile or adult *H. bivittatus*, there were significant effects on home range location. It appears that *H. bivittatus* requires a certain area for their home range, and although they are forced to relocate this home range, they maintain the same size of home range for foraging, microhabitat availability, or social purposes. The allometric relationship between total length of *H. bivittatus* and home range area appears to be unaltered by beaugregory introductions. One surprising result from this study is that after the introduction of beaugregories, despite the freedom and ability of all individuals to emigrate from their home range area to an entirely new area on the reef, all focal individuals maintained some portion of their original home range location. It appears that *H. bivittatus* are willing to tolerate beaugregory introductions as a trade-off to relinquishing all advantages of familiarity with a section of the reef (Reinboth 1973; Wootton 1990; Barrett 1995; Braithwaite 1998; Kramer and Chapman 1999).

General statement about interspecific competition

This study revealed significant effects for *H. bivittatus* due to interspecific interference competition. Agonistic encounters between the pomacentrid and the labrid resulted in adverse effects for the labrid. The adverse effects included significant increases in the amount of time involved in chases or aggressive actions by the beaugregories, which, for adult *H. bivittatus*, led to subsequent reductions in the amount of time spent foraging or in a foraging assemblage. However, there are statements in the literature about the importance of interspecific competition, or interspecific agonistic encounters that are not supported by this study. For example, Miller (1978)

stated that most agonistic situations occur among conspecifics and some researchers limit the concept to intraspecific encounters. The pomacentrid-labrid interaction described in the present study clearly contradicts this limit of agonistic interactions to intraspecific contenders. Schoener (1983) further stated that interspecific competition occurs most frequently among species that have high overlaps in diet and microhabitat use. This is also not the case for the relationships described in the present study for two reasons: 1) *H. bivittatus* are microhabitat generalists and their loose requirements for any type of microhabitat with structural complexity and a minimal area of sand alleviate a high degree of microhabitat overlap between *S. leucostictus* and *H. bivittatus*, and 2) *H. bivittatus* are opportunistic omnivores whereas *S. leucostictus* are predominantly herbivores.

Labrid-pomacentrid interactions

Many coral reef studies have used pomacentrids to investigate ecological processes in coral reef fish communities (Sale 1971; Clarke 1977; Itzkowitz 1977a,b; Thresher 1984; Ebersole 1985; Ferreira et al. 1998). Patterns of distribution and spatial dynamics have been fairly well documented for many pomacentrid species, and the present study investigated the effect of these ubiquitous and aggressive coral reef species on the non-territorial components of reef fish communities. Studies have shown that pomacentrids vary their level of aggression towards different species (higher aggression towards egg predators like labrids, and lower aggression towards wider roaming, herbivorous fishes like scarids and acanthurids) (Reinboth 1973; Myrberg and Thresher 1974; Katzir 1981; Ferreira et al. 1998). One reason why *H. bivittatus* may forage in large, mixed assemblages as it grows larger is to confuse the territorial pomacentrids that use species recognition to vary their levels of aggression against invading fishes. In fact, Lawson et al. (1999) found that schooling behaviour in acanthurids permits access to higher quality food in the territories of damselfish.

Effects of damselfish introductions on home range area and relocation

Beaugregory introductions caused *H. bivittatus* juveniles and adults to relocate their home ranges. This supports the growing body of literature that recognizes that territories and home ranges are not fixed parcels of real estate (Eifler 1996; for a review see Gordon 1997). The present study found evidence to support the idea that home range boundaries are continually adjusting as a result of behavioural interactions. There are few studies in existence that have explicitly addressed this idea. Although Jones (1984a) observed changes in spatial arrangements of fishes due to interspecific foraging associations and aggressive interactions, he suggested that these effects were probably transitory. However, he further stated that the home range or territory of an individual is likely to change as it grows, since it may become less dependent on shelter, as well as change its diet, and its response to other conspecific or heterospecific individuals. Although my observations only occurred over a period of weeks, the results suggested that there was a permanent shift after beaugregory introductions in home range use by *H. bivittatus*, as long as the introduced beaugregories were left in their new area. The complexity of the situation is increased by stating that damselfishes also show fluctuating territorial boundaries (Itzkowitz 1985; McGehee 1995). Itzkowitz (1985) investigated the instability in territory possession in the beaugregory damselfish, and he found that all individuals, regardless of sex and size class, made constant and unpredictable movements during his study. Additionally, McGehee (1995) found that adult beaugregories changed sites occasionally, which suggested that emigration is an important post settlement process. Beaugregory emigration did not occur during the experimental conditions for the present study, but in natural conditions, spatial dynamics and behavioural interactions are extremely dynamic processes.

Effects of damselfish introductions on microhabitat use, behaviours, and social interactions

Adult *H. bivittatus* were forced to use alternative microhabitats after beaugregories were introduced into their home ranges. This shift in microhabitat use is most likely obligatory, because the adults were forced to relocate their original home range area. In a previous study (Chapter V), it was found that *H. bivittatus* are microhabitat generalists, and do not show affiliations for any particular microhabitat features. Although beaugregory introductions did not result in large shifts in microhabitat use for juvenile *H. bivittatus*, there was a low degree of congruency in microhabitat use for the controls. This low degree of similarity in microhabitat use in juveniles could be a result of the relationship of the size of microhabitat patch relative to home range size. In other words, microhabitat patches may be large relative to the average home range size of $4.3 \pm 0.3\text{m}^2$. A subtle shift in coordinates of the juvenile may result in a marked change in the percentage of time spent in a particular microhabitat.

With respect to behaviours and social interactions, the most significant effects of beaugregory introductions were increased agonistic encounters between *H. bivittatus* and the introduced beaugregories. For adult *H. bivittatus*, this increase led to a reduction in the amount of time they could spend foraging or in a foraging assemblage. Juveniles appear to spread the resultant loss of time in their activity cycles among many different behaviours. Furthermore, because juvenile and adults interact differently with conspecifics, heterospecific labrids, acanthurids and scarids, there was no significant reduction in the amount of time juveniles spent in foraging assemblages after introductions of beaugregories.

A significant reduction in the amount of time adults spent in a foraging assemblage could adversely affect them not only by reducing foraging time, but also by decreasing the other advantages of being in a group (i.e. heterospecific social facilitation (Baird 1993)). Swimming or behaving in groups reduces the success of predators, increases foraging success, synchronizes

breeding behaviour, and increases hydrodynamic efficiency when swimming (Magurran 1990; Baird 1993; Helfman et al. 1997). Foragers in groups may locate food sooner, take food in faster, have more time available for foraging, or grow faster. The benefit increases with increasing shoal size (Helfman et al. 1997). Increasing benefits arise because a fish in a group can search for food while simultaneously watching for signs of successful feeding in groupmates, thus increasing the area over which it effectively searches. Also, the time each individual spends scanning for predators may decrease, leaving more time for feeding (Helfman et al. 1997).

Beaugregory introductions led to a decrease in the amount of time adults could spend interacting with scarids and acanthurids. This could be considered as an “interaction modification” (Adler and Morris 1994); whereby interspecific competition between the pomacentrid and labrid was the source of the interaction modification between labrids and scarids and acanthurids. Interaction modifications have been defined as direct pairwise interactions that are modified by the presence or density of other species (Adler and Morris 1994). Although this term was developed and applied in studies of predator-prey dynamics and complex food webs, the description clearly pertains to the suppression of time adult *H. bivittatus* spent with either acanthurids or scarids due to the increased densities of *Stegastes leucostictus*. Adler and Morris (1994) present a summary of the various views of communities: 1) assemblages of species with no direct interactions, 2) sets of species involved only in pairwise interactions that operate more or less independently, and 3) complex webs of action and reaction involving multiple species simultaneously. The present study is described by the third view of community structure because it involves complex dynamics between multiple species.

Effects of damselfish introductions on swimming distance above the substrate

Swimming distance above the substrate appears to be a very inflexible behaviour in *H. bivittatus*. Juveniles spent consistent amounts of time at different levels above the substrate, and

overall, tended to spend a greater amount of time closer to the substrate than adults. Adults also showed a high amount of consistency in their position above the substrate, and this pattern was not modified by the introduction of beaugregories. Swimming distance above the substrate is more rigid than some of the other behaviours and social interactions recorded. Rigidity in behaviours was also observed by Gutierrez (1996), who found that after settlement, despite the importance of microhabitat configuration on this behaviour, some species of pomacentrids were more rigid than others when it came to relocating into more favorable locations.

Post-recruitment processes and the fluid mosaic of individual home range boundaries on the reef

Patterns of distribution and abundance of coral reef fish depend in part on recruitment of a pelagic larval stage, subsequent dispersal and relocation among habitats, and survival of new recruits (Jones 1987). The present study looked at post-recruitment processes and found that interspecific competition between pomacentrids and labrids may influence the distribution of the labrid, *H. bivittatus*. There is evidence that distributions of adult and juvenile coral reef fishes can be modified by several post-recruitment processes, including behavioural interactions (Risk 1998), acquiring home range areas (de Martini 1998), and habitat availability (Caley and St John 1996). Risk (1998) found that post-settlement persistence of an acanthurid, *Acanthurus bahianus*, was negatively related to the level of aggression received from beaugregories. De Martini (1998) stated that in reef fishes differences in size-related patterns of movement, and in requirements for home range size importantly modify the effects of the recruitment process on population dynamics. Finally, Caley and St John (1996) found that patterns of recruitment with respect to species richness and abundance can be modified considerably over small spatial and temporal scales by differences in refuge availability.

Modeling spatial behaviour in coral reef fish: the next step

In the theoretical literature, many ways of modeling space use by individuals have evolved (Stamps et al. 1987; Holmes et al. 1994; Cantrell and Cosner 1999; McCarthy 1999). These models could very well be used in coral reef systems.

Depending on the arrival time and location of new settlers, they each encounter very different scenarios with respect to availability of suitable habitat, and configurations of neighbours. Holmes et al. (1994) used partial differential equations to model various ecological phenomenon including dispersal, diffusion-driven spatial patterning, and dispersal-mediated coexistence. Their models supported the idea that simple organism movement can produce striking large-scale patterns in homogeneous environments, and that in heterogeneous environments, movement of multiple species can change the outcome of competition and predation.

McCarthy (1999) presented an interesting way of modeling the effects of competition or space pre-emption on “natal” dispersal distance. Two types of dispersal away from “natal” location, are sequential dispersal and simultaneous dispersal (McCarthy 1999). Sequential dispersal occurs when an individual disperses only after the preceding disperser has settled. Simultaneous dispersal occurs where dispersers compete for vacancies, or suitable habitat, at the same time. These models appear to be very appropriate to the relocation possibilities for settlers, recruits, juveniles, and possibly even adults of coral reef fish species. The experimental approach taken in the present study may present one potential way of bridging the gap between empirical data and theoretical modeling of relocation and the spatial dynamics of populations such as that of McCarthy (1999).

An additional model was developed by Cantrell and Cosner (1999) that employed reaction-diffusion equations to show how behaviour of individuals at patch boundaries can be modeled when a bias exists in the direction an individual moves when it encounters an interface. Their

approach was similar to that of Stamps et al. (1987) who looked at “hard-edge” boundaries versus “soft-edge” boundaries. Although their models pertained to habitat quality, their boundaries could also represent social interactions. Hard-edge boundaries would be exemplified by a pomacentrid-labrid boundary, and a soft-edge boundary would be exemplified by a labrid-labrid boundary. These models are developing quite nicely in the theoretical sense, but empirical data are lacking and would be difficult to collect. However, it would be interesting to revisit the data presented in this paper by using them in these types of models so the unique configurations of microhabitats and surrounding neighbours, and behavioural patterns of each individual can be considered and applied towards a better understanding of the dynamics of coral reef fish communities.

Concluding statements

This study applied an experimental approach towards compiling a better understanding of coral reef fish dynamics. Insight has been gained into the importance of territoriality and agonistic interactions in affecting space use in non-territorial, wider-ranging foragers. Although *H. bivittatus* were very abundant in back reef areas of Tague Bay, other heterospecific labrids like *H. maculipinna*, *H. poeyi*, *H. garnoti*, and *H. radiatus* were not as abundant in this location. If these species are affected as dramatically as *H. bivittatus* due to introductions of *Stegastes leucostictus*, there may be greater consequences on their population demographics. This study has shown that interspecific competition between *S. leucostictus* and *H. bivittatus* causes changes in spatial dynamics, behaviours, and social interactions in juvenile and adult *H. bivittatus*.

Table 6.1. Amount of time spent doing common behaviours for juvenile and adult *Halichoeres bivittatus* prior to any manipulations. "Foraging" for juveniles consisted of eating + touching nose to substrate. "Foraging" for adults consisted of eating + touching nose to substrate + swimming with conspecifics and heterospecifics (either separately or combined). $n = 24$ fish.

JUVENILE BEHAVIOURS	Average % time spent doing behaviour before manipulation (\pm s.e.)	ADULT BEHAVIOURS	Average % time spent doing behaviour before manipulation (\pm s.e.)
"Foraging"	41.42 (0.97)	"Foraging"	40.73 (1.02)
touching nose to substrate	21.15 (0.82)	eating	20.21 (0.84)
eating	20.28 (0.90)	swimming alone	20.14 (0.98)
eye flicker	19.76 (0.90)	touching nose to substrate	13.16 (0.60)
swimming alone	8.16 (0.50)	"Bobbing"	8.30 (0.53)
damselfish chases	7.40 (0.48)	swimming with others	7.36 (0.53)
hovering	6.53 (0.39)	damselfish chases	7.08 (0.49)
"Bobbing"	3.92 (0.37)	hovering	5.17 (0.44)

Table 6.2. Effect of damselfish introductions on *Halichoeres bivittatus* behaviour. One way ANOVAs were done separately on each of the behaviours, and tested for differences in the % change in time spent doing the different behaviours following the manipulation (dependent variable). The ANOVAs tested for differences among all of the means of the control and treatment groups. (df = 3). Tukey's *post hoc* test of multiple comparisons followed any one-way ANOVA that yielded a significant difference. D = damselfish, T = tile

JUVENILE BEHAVIOURS	Between Groups SS	Between Groups MS	F	p	Multiple Comparisons
"Foraging"	1791.83	597.28	1.87	0.168	ns
touching nose to substrate	2053.65	684.55	1.16	0.349	ns
eating	2514.60	838.20	1.12	0.363	ns
eye flicker	18902.64	6300.88	2.92	0.059	ns
swimming alone	2945.83	981.94	0.90	0.456	ns
damselfish chases	83869.78	27956.59	19.76	<0.001	3D > 1T; 3D > 3T; 3D > 1T
hovering	4232.64	1410.88	0.57	0.642	ns
"Bobbing"	2516.94	838.98	0.38	0.770	ns

Table 6.2. (Continued)					
ADULT BEHAVIOURS	Between Groups SS	Between Groups MS	F	p	Multiple Comparisons
"Foraging"	1744.88	581.63	4.93	0.010	3D > 1T
eating	2826.67	942.22	1.24	0.323	ns
swimming alone	2306.50	768.83	0.58	0.633	ns
touching nose to substrate	2460.74	820.25	0.95	0.435	ns
"Bobbing"	9779.11	3259.70	1.16	0.348	ns
swimming with others	8351.61	2783.87	0.52	0.676	ns
damselfish chases	108869.76	36289.92	3.60	0.031	3D > 1T
hovering	22766.47	7588.82	2.20	0.119	ns

Table 6.3. Amount of time spent in social interactions for juvenile and adult *Halichoeres bivittatus* prior to any manipulations. n = 24 fish

JUVENILE interactions with:	% Time spent interacting before manipulation (\pm s.e.)	ADULT interactions with:	% Time spent interacting before manipulation (\pm s.e.)
Foraging assemblage	56.63 (2.37)	Foraging assemblage	56.15 (2.77)
<i>H. bivittatus</i> juveniles	32.26 (1.36)	<i>H. bivittatus</i> adults	20.52 (1.19)
Scarid juveniles	14.90 (1.19)	Scarid juveniles	11.63 (1.08)
<i>S. leucostictus</i> total	6.32 (0.44)	<i>H. bivittatus</i> juveniles	9.90 (0.79)
<i>H. bivittatus</i> adults	6.11 (0.83)	<i>S. leucostictus</i> total	6.39 (0.48)
<i>S. leucostictus</i> adults	3.33 (0.44)	Acanthurid juveniles	5.83 (0.69)
<i>S. leucostictus</i> juveniles	3.02 (0.37)	<i>S. leucostictus</i> adults	5.17 (0.46)

Table 6.4. Effect of damselfish introductions on social interactions of *Halichoeres bivittatus*. One way ANOVAs were done separately on each of the social interactions, and tested for differences in the % change in time spent with each species or groups of species before versus after the manipulation (dependent variable). The ANOVAs tested for differences among all of the means of the control and treatment groups. (df = 3). Tukey's *post hoc* test of multiple comparisons followed any one-way ANOVA that yielded a significant difference. Multiple comparison numbers correspond to the following treatments: 1= 0 damselfish, 1 tile; 2= 0 damselfish, 3 tiles; 3= 1 damselfish, 1 tile; 4= 3 damselfish, 3 tiles.

JUVENILE interactions with:	Between Groups SS	Between Groups MS	F	P	Multiple Comparisons
Foraging assemblage	4700.48	1566.83	2.00	0.147	ns
<i>H. bivittatus</i> juveniles	3611.388	1203.80	1.637	0.213	ns
Scarid juveniles	6815.65	2271.88	0.85	0.481	ns
<i>S. leucostictus</i> total	131008.90	39377.01	19.59	<0.001	4 > 1; 4 > 2; 4 > 3
<i>H. bivittatus</i> adults	6332.99	2111.00	0.82	0.498	ns
<i>S. leucostictus</i> adults	467089.09	155696.36	12.01	<0.001	4 > 1; 4 > 2; 4 > 3
<i>S. leucostictus</i> juveniles	100170.84	33390.28	0.78	0.519	ns
ADULT interactions with:					
Foraging assemblage	9870.88	3290.29	9.82	<0.001	1 > 3; 1 > 4; 2 > 3
<i>H. bivittatus</i> adults	9739.31	3246.44	1.13	0.362	ns
Scarid juveniles	26701.36	8900.45	8.27	<0.001	2 > 4; 2 > 3; 1 > 4; 1 > 3
<i>H. bivittatus</i> juveniles	12325.08	4108.36	1.39	0.281	ns
<i>S. leucostictus</i> total	160612.12	53537.38	10.12	<0.001	4 > 1, 4 > 2, 3 > 1, 3 > 2
Acanthurid juveniles	34302.96	11434.32	5.73	0.005	1 > 4; 1 > 3
<i>S. leucostictus</i> adults	186907.77	62302.59	10.87	<0.001	4 > 1, 4 > 2, 3 > 1, 3 > 2

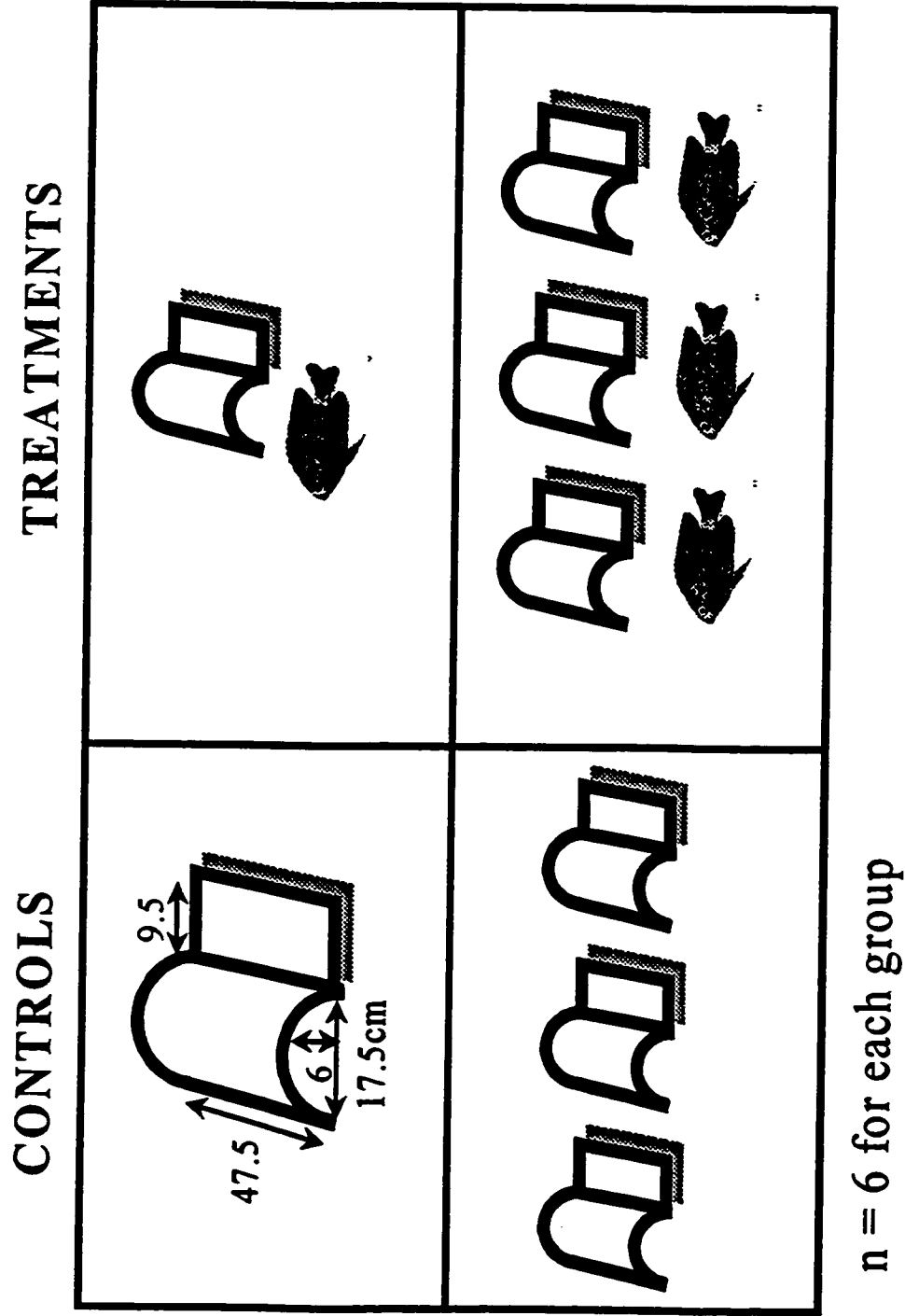


Figure 6.1. Diagram of experimental design. The dimensions for the artificial shelters (terracotta roofing tiles) are given in cm and are not drawn to scale.

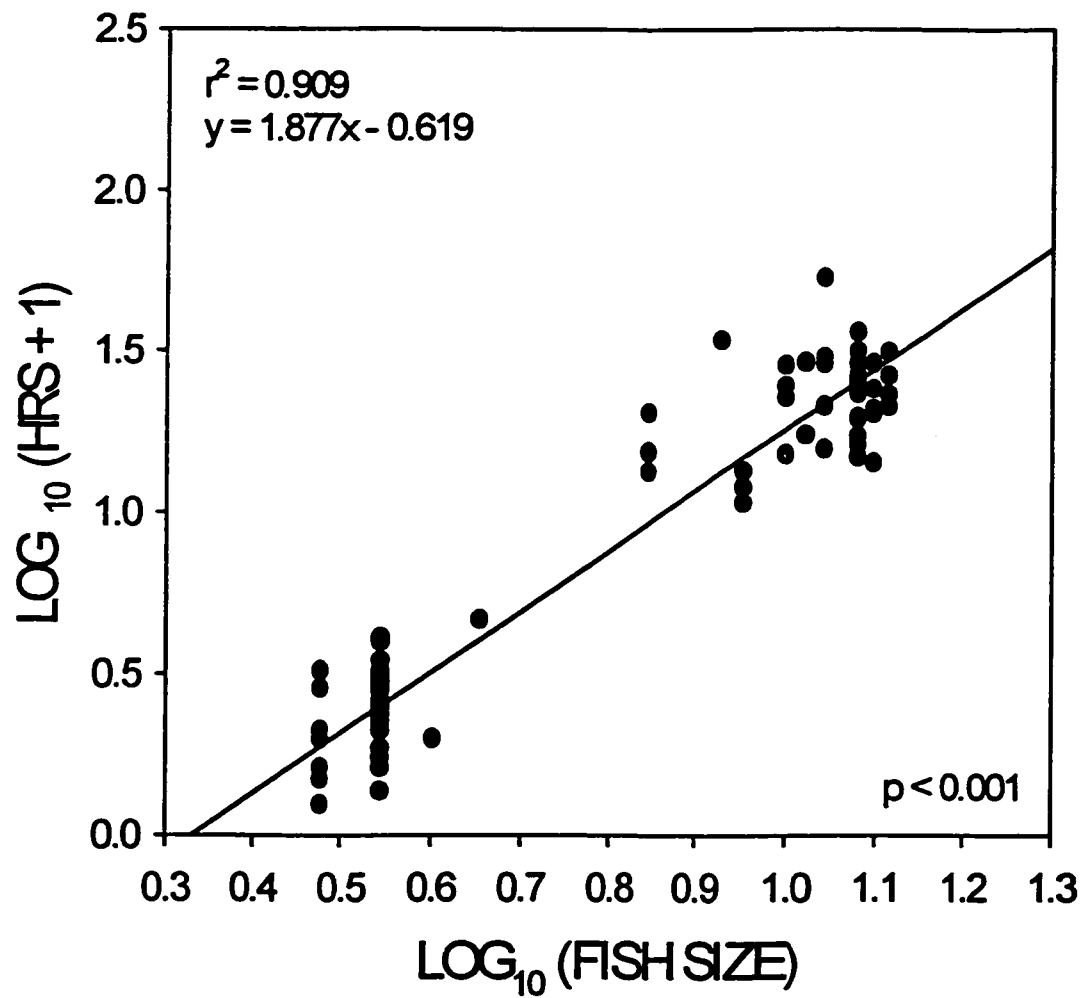


Figure 6.2. Relationship of $\log_{10}(\text{home range size} + 1)$ to $\log_{10}(\text{fish total length})$ for *Halichoeres bivittatus*. $n = 77$ individual fish; 48 were focal individuals for the experimental manipulations and 29 were additional individuals observed in a preliminary study.

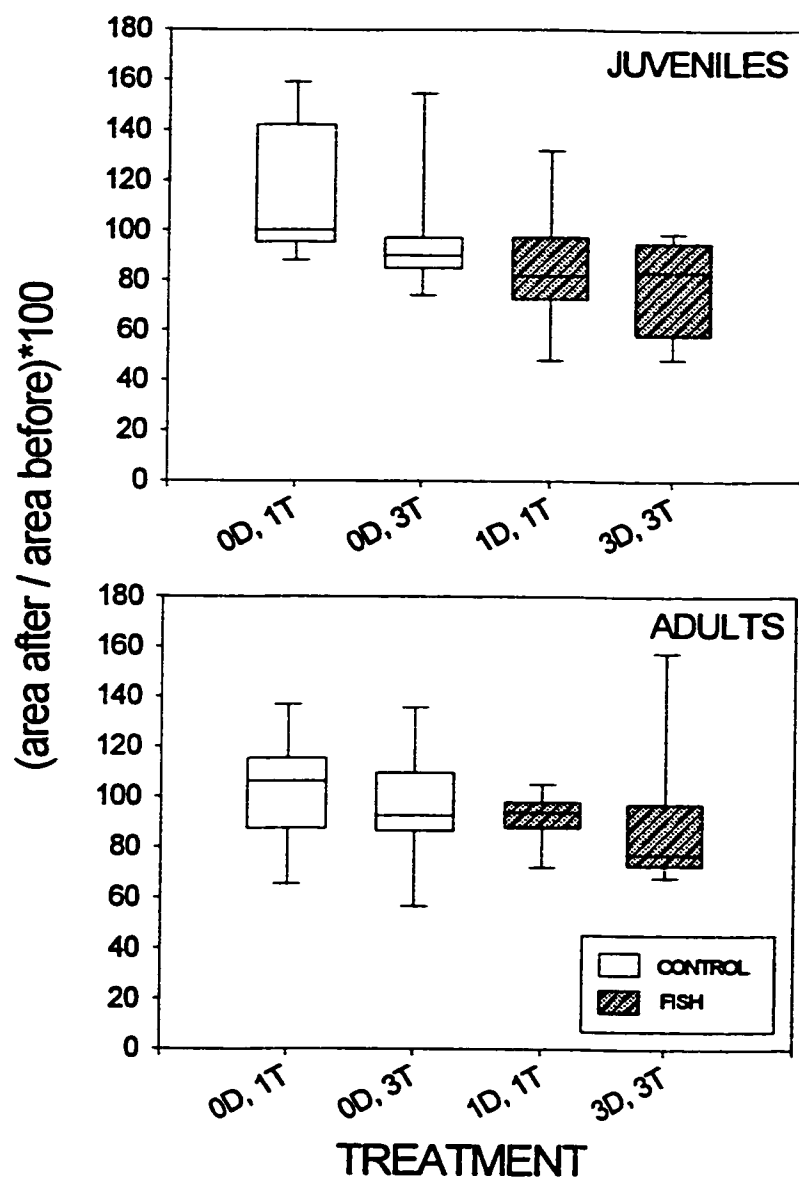


Figure 6.3. Ratio of home range area after the manipulation versus before (mean, 95% C.I., and st. dev.). There were no significant differences among the controls or treatment groups. $n = 6$ replicates per box; D = damselfish, T = tile.

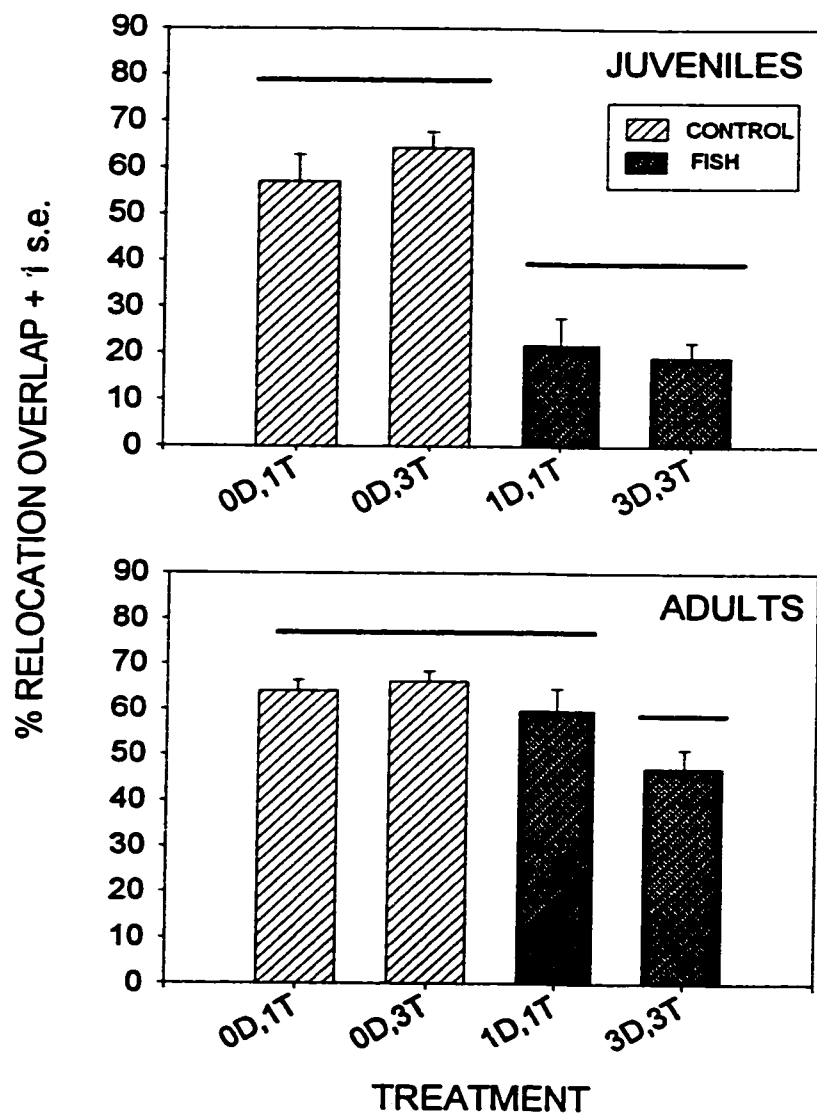


Figure 6.4. Percentage overlap (+1 s.e.) of home range position before and after the manipulation. Lines above the bars represent no significant differences among the groups ($p > 0.05$). Lines that are separated represent significant differences ($p < 0.05$). $n = 6$ replicates per bar; D = damselfish, T = tile.

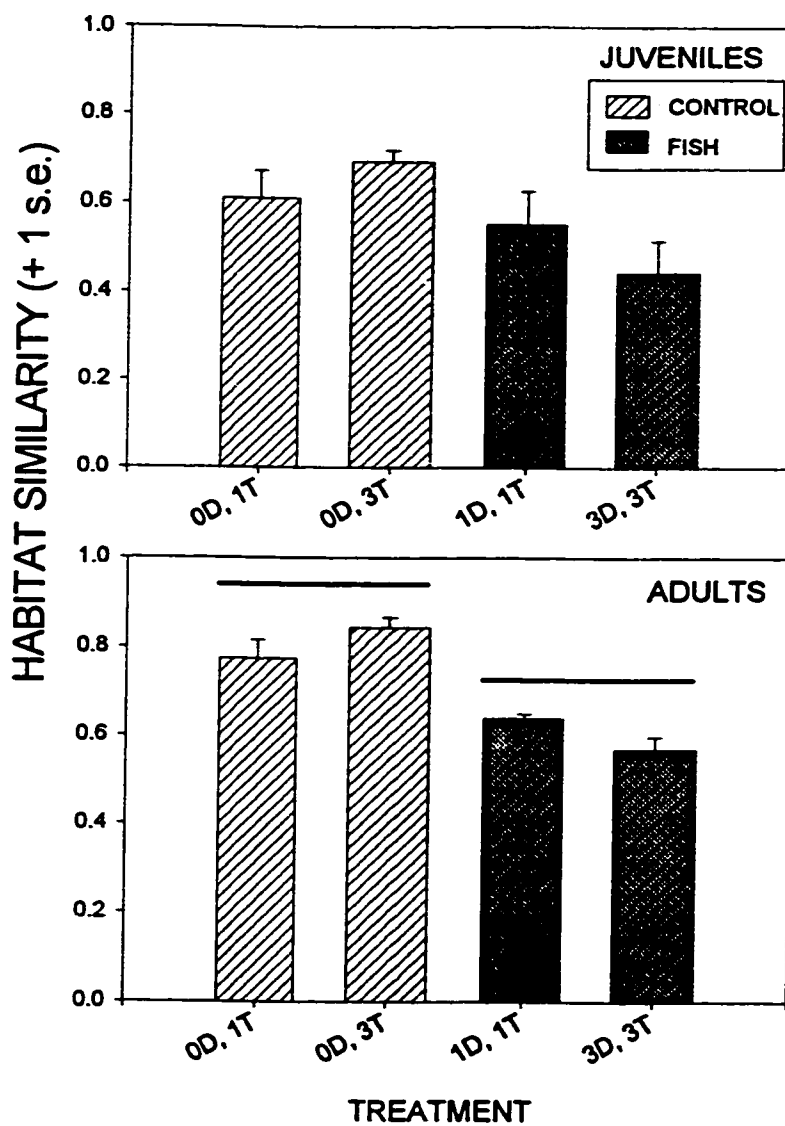


Figure 6.5. Proportional similarity in habitat use before and after the manipulation (+ 1 s.e.). Lines above the bars represent no significant differences among the groups ($p > 0.05$). Lines that are separated represent significant differences ($p < 0.05$). $n = 6$ replicates per box; D = damselfish, T = tile.

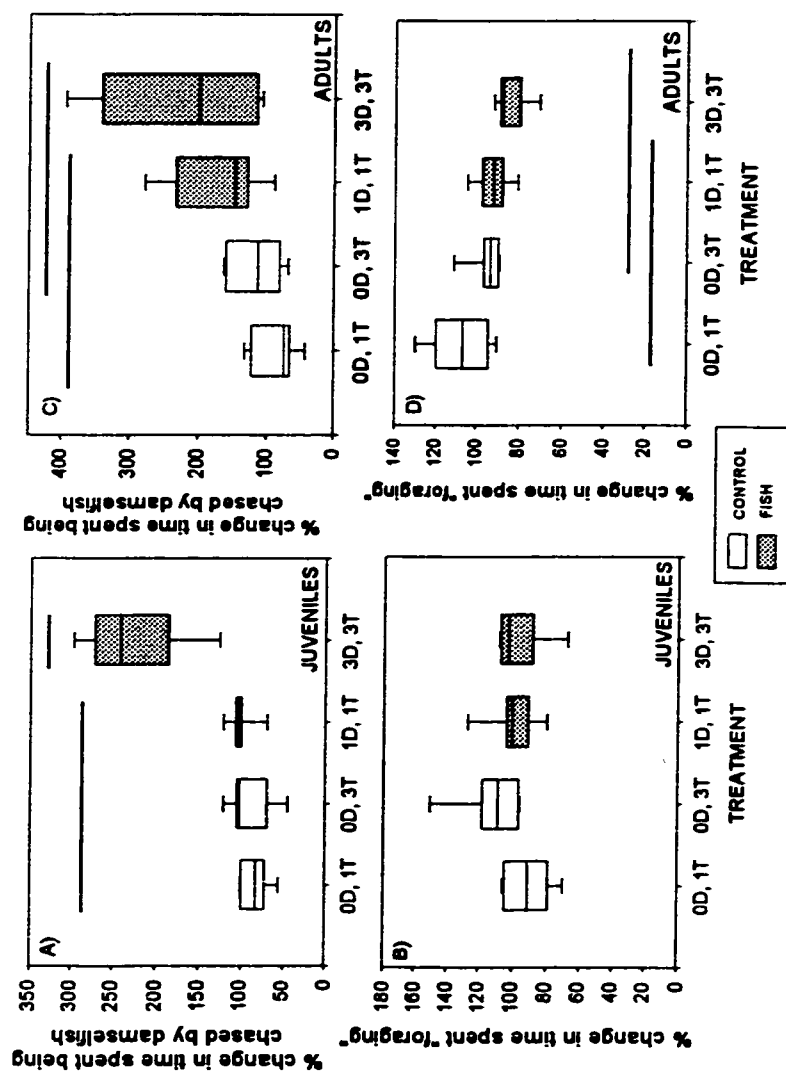


Figure 6.6. Effects of experimental manipulations on behavioural time budgets for *Halichoeres bivittatus*. Boxes A) and B) represent the % change in time juveniles spent being chased by damselfish or foraging, respectively (mean, 95% C.I., and st. dev.). Boxes C) and D) represent the % change in time adults spent being chased by damselfish or foraging, respectively. Lines above the bars represent no significant differences among the groups ($p > 0.05$). Lines that are separated represent significant differences ($p < 0.05$). $n = 6$ replicates per box; D = damselfish, T = tile.

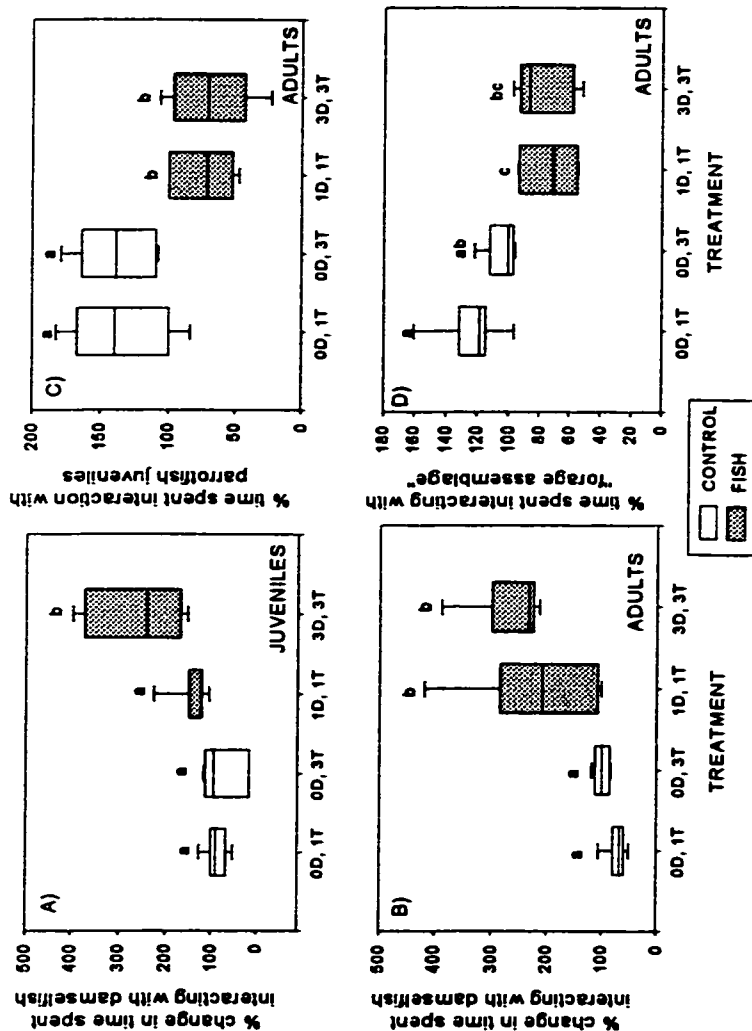


Figure 6.7. Effects of experimental manipulations on social interactions for *Halichoeres bivittatus*. Boxes A) and B) represent the % change in time spent interacting with damselfish for juveniles and adults, respectively (mean, 95% C.I., and st. dev.). Boxes C) and D) represent the % change in time adults spent interacting with parrotfish juveniles or a "foraging assemblage", respectively. Common letters above the bars represent no significant differences among the groups ($p > 0.05$). Bars that do not share a common letter are significantly different ($p < 0.05$). $n = 6$ replicates per box; D = damselfish, T = tile.

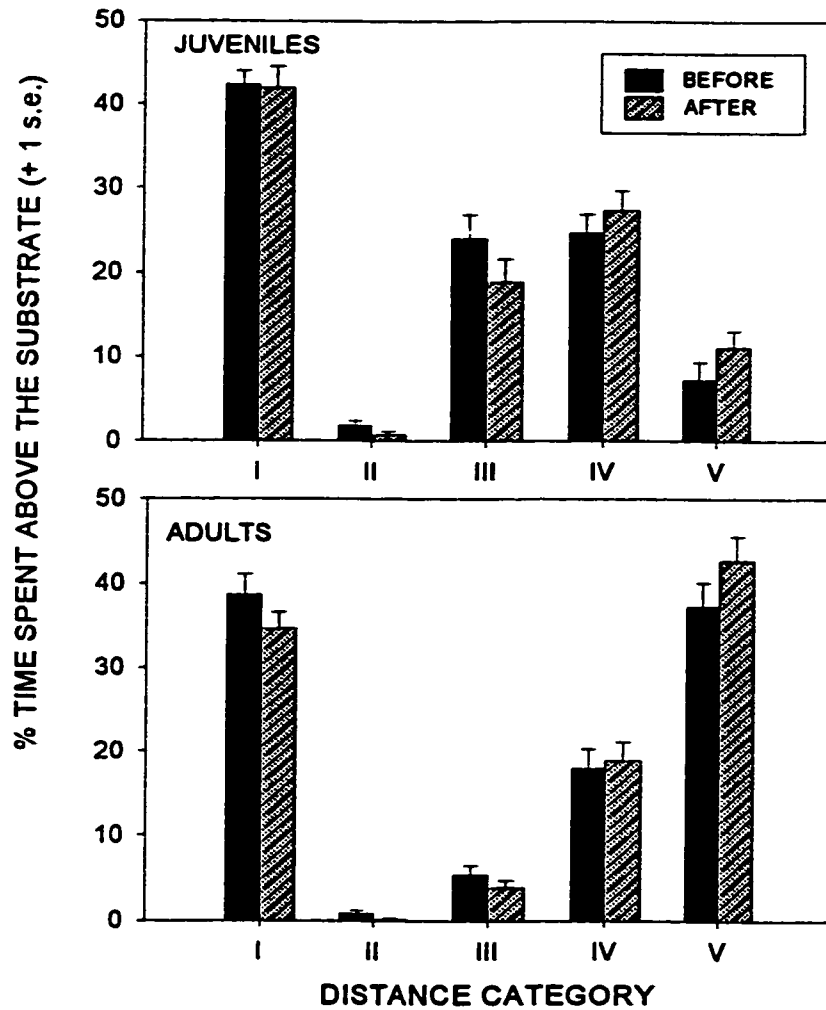


Figure 6.8. Effects of introducing 3 damselfish into the center of adult home ranges or adjacent to juvenile home ranges on swimming distance above the substrate. Dark bars represent mean % of time (+ 1 s.e.) spent in each distance category before the addition of damselfish, and light bars represent after.

CHAPTER VII

ENVIRONMENTAL FACTORS AFFECTING LABRID DISTRIBUTION

ABSTRACT

Spatial variability in assemblages of labrids was investigated on continuous coral reefs in St. Croix, U.S.V.I. Juveniles, intermediate phase (IP) adults, and terminal phase (TP) adults of six labrid species (*Halichoeres bivittatus*, *H. garnoti*, *H. maculipinna*, *H. poeyi*, *H. radiatus*, and *Thalassoma bifasciatum*) were visually censused along strip transects at eight different locations. Relationships between labrid abundances and environmental variables were investigated using Canonical Correspondence Analysis. It was found that zonation is a primary factor that affects assemblage structure of these Caribbean labrids, due to higher abundances of *Halichoeres bivittatus* and *H. poeyi* in the back reef zone than the fore reef zone, and higher abundances of *Thalassoma bifasciatum* in the fore reef zone. *Halichoeres garnoti*, and *H. maculipinna* do not show great degrees of differences in abundance between the back reef and fore reef zones. *H. radiatus* was the rarest labrid included in this study, but showed comparable numbers on back reef and fore reef sites. Additional to zonation, environmental variables that were hypothesized to affect labrid assemblage structure included depth, topographic complexity, microhabitat availability, and the abundances of territorial damselfish species. After separating back reef and fore reef data, analyses revealed several relationships between labrids and environmental variables. Topographic complexity and depth within zones did not exert significant effects on labrid assemblage structure. On the back reef, *H. maculipinna* juveniles, *H. poeyi* juveniles and IP

adults, and *H. bivittatus* juveniles and IP adults were all negatively associated with adult beaugregory damselfish. With damselfish removed from the environmental variables in the back reef data set, strong associations became apparent between *H. bivittatus* IP adults and algae on sand, *H. bivittatus* juveniles and sand, and *H. garnoti* TP adults and sand. The biological associations between labrid variables and environmental variables for the fore reef data set were not as easily interpretable. This is probably due to the dominance of *Thalassoma bifasciatum* on fore reef habitats. This species is a zooplanktivore and is predominantly found in large schools of conspecifics in the fore reef zone, suggesting very low biological associations with the particular microhabitat features included in this study.

INTRODUCTION

One central question in ecology is what organizes or regulates community structure (Hairston et al. 1960, Connor and Simberloff 1979, Sugihara 1980, Grossman 1982). Factors that influence community structure appear to be similar in different systems, but the degree to which these factors affect the community is system-specific. For marine organisms with complex life histories, many researchers now recognize that the interplay of numerous factors causes pre-settlement losses of larvae and post-settlement losses of juveniles (Doherty 1991, Jones 1991, Doherty and Fowler 1994). For reef fishes, researchers have demonstrated that stochastic variation in larval success can affect recruitment strength (Williams and Sale 1981, Sale et al. 1984, Doherty 1987), but that high juvenile mortality can also modify recruitment patterns (Doherty and Sale 1985, Victor 1986, Eckert 1987, Shulman and Ogden 1987, Meekan 1988, Robertson 1988).

Individuals or groups of individuals are not scattered randomly about the reef environment, but rather their distribution reflects both topographic and biological features of the reef as well as

the specific biotic requirements and social interactions of the fishes (Thresher 1977, Matthews 1998). The consequences of differential use of patches by individual organisms and environmental heterogeneity have received increasing interest by terrestrial and marine ecologists (Sale 1977, Gladfelter and Gladfelter 1978, Sousa 1984, Behrens 1987, Anderson et al. 1989, Connell and Jones 1991, Moller 1991, Buchheim and Hixon 1992, Crowe 1996). Chapter V considered the microhabitat requirements of these six labrids used in the present study and found microhabitat selectivity among the species and their life stages. For example, as these labrids grow, they increase their use of topographically simple microhabitats. Additionally, several species showed preference for particular microhabitats, such as *Halichoeres bivittatus* associated with sand microhabitats, and *H. poeyi* with algae on coral rubble. Do these preferences for small patches within their home range areas result in detectable associations between species abundances and microhabitat availability on larger spatial scales?

Ecologists are constantly struggling with the issue of spatial scale in their research, as we realize how critical it is to ask appropriate questions for the level of investigation (Doherty 1987, Menge and Olson 1990, Caley 1995, Meekan et al. 1995). Habitat selection occurs over a range of spatial scales, from the geographic range of a species, to individual home ranges within a geographical range, to use of general features within the home range, to the selection of particular elements within the general features (Manly et al. 1993).

On spatial scales at the level of entire reefs, many fishes segregate by reef zones, and thus can often be characterized by depth or zone preferences (Fishelson et al. 1974, Clarke 1977, Bouchon-Navaro and Harmelin-Vivien 1981, Williams and Hatcher 1983, Russ 1984, Alevizon et al. 1985, Macpherson 1994, McCormick 1994). This pattern has also been observed in labrids (Warner and Robertson 1978, Green 1996). For seven of the abundant labrid species studied by Green (1996) on the Great Barrier Reef, depth appeared to be of overriding importance in

determining habitat use, with most species occurring either in shallow or deep zones. In her study, no clear relationship was detected between labrid density or diversity and other habitat features such as percentage living substratum, substratum diversity, or complexity.

Other species of coral reef fish have demonstrated associations with particular kinds of microhabitat. However, many contrasting patterns in the relationships between fish communities and coral cover, habitat heterogeneity, or topographic complexity have been described, including strong positive or negative effects of particular habitat characteristics (e.g. Risk 1972, Nagelkerken 1977, deBoer 1978, Carpenter et al. 1981, Bell and Galzin 1984, Bell et al. 1985, Findley and Findley 1985, Bouchon-Navaro and Bouchon 1989, Grigg 1994, Jones and Kaly 1995, Hart et al. 1996, Jennings et al. 1996) as well as those finding weak or no relationship (Roberts and Ormond 1987, Roberts et al. 1988, Fowler 1990, Booth and Beretta 1994, Cox 1994, Green 1996). The establishment of correlations between topographic complexity or other habitat characteristics and the diversity of reef fish assemblages indicates that reef fish populations respond to the physical nature of the substratum (reviewed in Connell and Jones 1991).

In addition to reef zones and microhabitat characteristics, social interactions with other fishes may also affect the distribution of the labrids included in this study. Few studies have investigated the effect of behavioural interactions on spatial dynamics (but see Jones 1984a, Itzkowitz 1977b, Coleman and Wilson 1996). One study by Jones (1984a) suggested that aggressive interactions and interspecific foraging associations influenced the behaviour and use of space by the temperate labrid, *Pseudolabrus celidotus*. However, he inferred that these activities probably only had a transitory influence on the spatial distribution of this wrasse. Itzkowitz (1977b) observed that uni-specific adult colonies of Caribbean pomacentrids were a result partly due to a behavioural system which inhibits other species from sharing a common territorial border on a homogeneous substratum. In a Chapter VI, results from experimental introductions of

beaugregory damselfish into the centers of home ranges occupied by *H. bivittatus* suggested that aggressive interactions with beaugregorys affected individual space use in *H. bivittatus*. These interactions were consequently hypothesized to affect the spatial distribution of *H. bivittatus* populations. Thus damselfish species were censused and included as environmental variables to determine their effect on labrid distribution at spatial scales larger than individual home ranges.

The general aim of this study was to determine environmental factors that affect labrid assemblage structure. Reef characteristics that were included as environmental factors in the analyses consisted of: 1) reef zone, 2) depth within a zone, 3) microhabitat availability, 4) topographic complexity, and 5) population abundances of territorial damselfish species. Through visual censuses and quantification of environmental parameters, general differences in labrid assemblage structure and environmental effects were determined. Canonical Correspondence Analysis was then used to determine the degree of association between patterns of abundance of labrid species and their life stages, and environmental parameters.

METHODS

Study animals

Juveniles, initial phase (IP), and terminal phase (TP) adults of the following labrid species were visually censused: *Halichoeres bivittatus*, *H. garnoti*, *H. maculipinna*, *H. poeyi*, *Thalassoma bifasciatum*. For the purpose of this study, counts of juveniles included recruits (i.e. juveniles = any fish < 30mm). There is considerable difference in color among these labrids as well as among the life stages within species. Colour pattern often provided good indication of life stage within these species (Roede 1972, Warner and Robertson 1978). Juveniles and IP adults are easily distinguishable for *H. garnoti* and *H. radiatus*. For *H. bivittatus*, *H. maculipinna*, *H. poeyi*, and *Thalassoma bifasciatum* juveniles were ≤ 30 mm in total length (c.f. Warner and Robertson 1978).

Terminal phase individuals were easily distinguished from IP and juveniles in all of the species because of their bolder colour patterns (except *Halichoeres poeyi*), and changes in morphology.

Fish censusing and quantification of environmental parameters

To investigate the degree of temporal and spatial variability in labrid abundances, visual censuses were conducted at permanent and temporary sites around St. Croix (Fig. 7.1.). Due to accessibility, permanent transects were set up at six sites of Tague Bay, with three sites located on the fore reef, and three sites on the back reef (Fig 7.1 and 7.2.). At these sites, eight permanent transects (30m x 1m) that ran parallel to the reef crest were marked with flagging tape. All eight transects were censused on two consecutive days which were considered replicate censuses, and 6-7 sets of censuses were completed during both 1997 and 1998. However, for the purpose of this study, all census days were averaged within a year. The degree of temporal variability (i.e. within a year) in labrid abundances at these sites will be considered in a separate study.

Temporary sites that were not as accessible as the permanent study sites were occasionally sampled during each field season. The two temporary sites included were Cane Bay on the northwestern shore of St. Croix, and South Shore, located on the southeastern shore of St. Croix (Fig. 7.2.). Only six transects were completed during each visit to these locations. The number of censuses completed at each site during the summers of 1997 and 1998 are combined and presented in Table 7.1. All juvenile, IP adult, and TP adult labrids 2 meters in front of the observer were recorded while swimming at a constant rate along the transects. The same transects were used in 1997 and 1998 at the Tague Bay sites, however, it was difficult to place the temporary transects at the same location during different visits to Cane Bay and South Shore.

To determine how much of the variation in labrid assemblage structure can be explained by environmental variables, several features of the reef habitat and its inhabitants were quantified, including: 1) depth, 2) microhabitat availability, 3) topographic complexity, and 4) number of

damselfish present. Damselfish (family Pomacentridae) are abundant on Caribbean reefs, highly territorial, and aggressive towards labrids, and were thus hypothesized to affect the distribution of labrids at these study sites. In Chapter VI, an experimental investigation on the effects of the beaugregory damselfish on one labrid species, *Halichoeres bivittatus*, determined that beaugregories affected the spatial positioning of this labrid on a small spatial scale (i.e. that of the home range). This study looks at possible larger scale effects of pomacentrid abundance on patterns of labrid distribution.

At each site, depth was recorded every 3 m along each transect, for a total of ten depth measurements per transect. Therefore, sixty to eighty depth measurements were taken for each site. These depth measurements are presented as an average depth per site.

Topographic complexity was measured using a profile gauge modified from a design by McCormick (1994). The profile gauge is constructed with a series of eleven vertical rods marked at increments of 0.5cm that easily slide up and down a horizontal bar for height adjustment. The rods are 1m in length and are placed 10cm apart. There is a carpenter's level on the apparatus that ensures the rods are always perpendicular to the ground. After the rods are fitted against the contour of the reef, the heights of each rod are recorded. The greater the difference in height between the rods, the higher the variance, which was termed the degree of topographic complexity. The profile gauge was used to quantify topographic complexity at five points along each transect. These measurements are presented as average topographic complexity within a site.

Microhabitat availability was also quantified at each site. Major substratum types were recorded every 25 cm along the transect, and they consisted of: 1) *Acropora palmata* rubble, 2) live *Porites porites*, 3) *Porites porites* rubble, 4) live *Montastrea annularis*, 5) *Montastrea annularis* rubble, 6) algae growing on coral rubble, 7) algae or isolated seagrass blades surrounded by sand, 8) small, unidentifiable pieces of coral rubble, 9) other live coral species,

10) gorgonians, 11) sea fans, 12) sponges, 13) sand, 14) pavement- hardened, planar surfaces of coral sometimes covered in a thin layer of sand, 15) *Porites astreoides*, 16) *Agaricia* spp., 17) *Millepora complanata*, 18) *Siderastrea siderea*, 19) *Diploria* spp., 20) seagrass (most commonly *Thalassia testudinum*), 21) other. The proportion of microhabitat available on all transects for each microhabitat category was pooled within a site for visual presentation. For statistical analysis, only the eleven most common microhabitats were included, based on average proportion coverage of > 2.5%. They consisted of the following: *Acropora palmata* rubble, live *Porites porites*, *P. porites* rubble, live *Montastrea annularis*, *M. annularis* rubble, algae on coral rubble, algae on sand, small coral rubble, pavement, sand, and other live coral species summed together (*Diploria* species, *Agaricia* species, *Siderastrea siderea*, and *Porites astreoides*).

To determine the effect of damselfish distribution and abundance on labrid assemblage structure, juveniles and adults of territorial damselfish species were censused along a second pass of the same transects used for labrid censusing. The following damselfish were counted (see Table 7.2. for maximum total lengths and depth preferences): beaugregory damselfish (*Stegastes leucostictus*), bicolor damselfish (*S. partitus*), cocoa damselfish (*S. variabilis*), dusky damselfish (*S. dorsopunicans*), longfin damselfish (*S. diencaeus*), threespot damselfish (*S. planifrons*), and yellowtail damselfish (*Microspathodon chrysurus*). They are all territorial and scrape algae off the surface of coral rubble for food. Some species may occasionally feed on plankton or benthic invertebrates (Bohlke and Chaplin 1968, Allen 1991). Only juveniles and adults of the four most common damselfish were included in the statistical analyses, and these consisted of beaugregorys, bicolors, duskys, and threespots. Cocoa, longfin, and yellowtail damselfish were not very common relative to the other species.

Statistical Analysis

Correlations between spatial patterns of labrid distribution and environmental parameters were determined using the Canonical Correspondence Analysis (CCA) proposed by terBraak (1986). All analyses were done using STATISTICA® software. CCA is a multivariate technique of direct gradient analysis that selects the linear combination of environmental variables that maximizes the dispersion of the species scores (Tabachnik and Fidell 1989). It chooses the best weights for the environmental variables to construct the first CCA axis (= Root 1). The second and further CCA axes also select linear combinations of environmental variables that maximize the dispersion of the species scores, but subject to the constraint of being uncorrelated with previous CCA axes. CCA has been used previously to correlate fish species distribution and environmental factors (Gomez et al. 1988, Adjeroud et al. 1998, Tejerina-Garro et al. 1998, Chittaro 2000). The following eighteen independent variables were included: zonation (back reef or fore reef), topographic complexity, depth, proportion availability of the following microhabitats: *Acropora palmata*, live *Porites porites*, *P. porites* rubble, live *Montastrea annularis*, *M. annularis* rubble, algae on coral rubble, algae on sand, small coral rubble, pavement, sand, the sum of live corals, and juvenile and adult abundances of the four following damselfish species: bicolor, beaugregory, dusky, and threespot. In order to improve linearity and homogeneity of variances, the proportions of microhabitat availability were angular transformed prior to analysis, and the labrid and damselfish counts were $\log_{10}(x + 0.5)$ transformed prior to analysis. The statistical unit for the CCA (or row) was one transect, with each column representing separate labrid and environmental variables.

From the CCA, factor loadings for environmental variables greater than $|0.3|$ suggest that the variable explains a reasonable portion of the relationship (Jongman et al. 1987, Tabachnik and Fidell 1989). These environmental variables are represented by vectors in the ordination plot

derived from the first two roots of the CCA. The longer the vector, the greater the relationship between that environmental variable and labrid variation. Life stages and species of labrids positioned close to an environmental vector have a strong relationship with that environmental variable. Variance extracted refers to the proportion of variance that a pair of canonical variates extracts from its own data set, and redundancy refers to the proportion of variance of one data set explained by the other data set (Tabachnik and Fidell 1989).

RESULTS

Labrid distribution and abundance

Many differences were found when comparing the distribution and abundance of labrid species at the different sites (Figs. 7.3-7.8). For some species, there were also differences between the two years at some sites. *Halichoeres bivittatus* were found in high numbers in the back reef sites and were the most common labrid at these locales (Fig. 7.3). *Halichoeres bivittatus* were rarely censused on fore reef sites. They showed lower recruitment during 1998 compared with 1997. Furthermore, within a year, overall abundances (juveniles, IP adults and TP adults considered together) were different among the sites, but the order was not consistent.

Halichoeres garnoti had higher numbers of recruits at Cane Bay compared to the other sites in both 1997 and 1998 (Fig. 7.4.). They were absent from South Shore censuses except for counts of a few recruits in 1998. Among the Tague Bay back reef and fore reef sites, the overall abundances of *H. garnoti* were similar. Within a site across years, the overall abundance of *H. garnoti* was also similar.

Halichoeres maculipinna showed higher levels of recruitment in 1998 at all sites (Fig. 7.5.). Recruitment levels were also higher at the back reef sites compared to the fore reef sites. Overall abundances were higher on the back reef sites than the fore reef sites.

Halichoeres poeyi showed higher levels of recruitment in 1997 than 1998, and higher overall abundances on back reef sites than fore reef sites (Fig. 7.6.). *Halichoeres poeyi* were rarely observed on fore reef sites. Sites TB4 and TB5 on the back reef of Tague Bay had higher overall abundances than TB6 and the South Shore site.

Halichoeres radiatus was the rarest labrid in this study. They were found in low numbers in both fore and back reef sites (Fig. 7.7.). Slightly higher levels of recruitment of *H. radiatus* were observed on the back reef sites. Very few juveniles or IP adult *H. radiatus* were observed at Cane Bay. Over the two summers of censusing, IP adults and TP adults were occasionally observed, but TP adults were never observed on a transect while censusing.

Thalassoma bifasciatum was the most common labrid on the fore reef sites. They were also found in high numbers on the back reef sites (Fig. 7.8.). Extremely high numbers of recruits were observed at Cane Bay compared to all other sites, and higher levels of recruitment were observed on the South Shore site compared to Tague Bay sites.

Quantification of environmental parameters

Fore reef sites were between 5 and 7m deep and back reef sites were between 1.3 and 1.6m deep (Table 7.3). Based on the results from the profile gauge measurements (Table 7.3), the fore reef sites and the most eastward back reef site of Tague Bay, (TB6) have greater degrees of topographic complexity than the other two back reef sites. Qualitative observations of high topographic complexity from large broken corals (*Acropora palmata*), and large mounds of *P. porites*, at TB6, compared with plains of algal turf and small coral rubble at TB4 and TB5, supported the measurements recorded with the profile gauge.

The sites differed in microhabitat composition (Fig.7.9). The fore reef sites of Tague Bay were more similar in composition to each other than to Cane Bay. The microhabitat category with the highest proportion at Cane Bay was 'other', and at this location, 'other' was dominated by

large mounds of brain coral rubble. The three fore reef sites at Tague Bay varied in the relative proportions of microhabitats, but all three have high proportions of *A. palmata* rubble, live *P. porites* and *P. porites* rubble.

The three back reef sites of Tague Bay were somewhat similar in microhabitat composition (Fig. 7.9.). *Acropora palmata* rubble, algae on coral rubble, and small coral rubble featured prominently at these sites, and TB6 also had many large mounds of *P. porites* rubble. The South Shore site was dominated by small coral rubble and *A. palmata* rubble, with very small proportions of the other microhabitats.

Damselfish abundances also varied among the study sites and across the years (Figs. 7.10.-7.13.). The greatest difference in damselfish distribution is between the two reef zones, with some species showing higher abundances on fore reef sites, and other species showing higher abundances on back reef sites. The dusky damselfish, *Stegastes dorsopunicans*, was very common on fore reef and back reef sites in both 1997 and 1998, although it was found in higher numbers on the fore reef sites (Fig. 7.10.). Very few juveniles were observed in either year, which remains a curiosity because adult dusky are so common in these locations. The beaugregory damselfish, *S. leucostictus*, exhibited lower levels of recruitment and abundances on the fore reef sites (Fig. 7.11.). Similar levels in recruitment and overall abundances were observed on the back reef sites over both years, with the exception of TB6 in 1998. The bicolor damselfish, *S. partitus*, had higher levels of overall abundance on fore reef sites (Fig. 7.12.). The numbers of bicolors varied within sites between years, and the rank order of abundances among sites was not consistent. Similarly, the three-spot damselfish, *S. planifrons*, had higher numbers on the fore reef sites. On the back reef, only TB6, had comparable abundances of three-spots compared with the fore reef sites. There were only a few three-spots observed at Cane Bay and South Shore.

Correlations of labrid distribution with environmental factors

The results of the CCA were greatly influenced by the combination of environmental variables included in the model. When reef zone was included as an environmental variable, higher proportions of variation in labrid variables were explained by the model (e.g. 34.4% with damselfish included as environmental variables, and 33.9% when damselfish were excluded from the model). Furthermore, the loadings for zone totally outweighed any of the other environmental variables. For example, when zone was included and all other environmental variables were included, the loading for Zone on Root 1 was -0.640, and Root 2 = 0.800. When zone was included and all other environmental variables were included except damselfish abundances, the factor loading for zones on Root 1 was -0.759, and Root 2 was 0.922.

Due to this overwhelming effect of zone on explaining labrid distribution, the data were analysed further within reef zones (Table 7.4). Two separate analyses were conducted with back reef data, and two analyses with fore reef data. The first analysis for each zone included all environmental variables, and the second set excluded damselfish abundances from environmental variables.

For the back reef data set with damselfish included as environmental variables, 21.8% of the variation in labrid variables was explained by the environmental variables, and the eigenvalues for Root 1 and Root 2 were both high (0.744 and 0.449, respectively) (Table 7.4). From the ordination plot (Fig. 7.14), *Halichoeres poeyi* juveniles and IP adults were closely associated with *P. porites* rubble. *H. maculipinna* juveniles, *H. poeyi* juveniles and IP adults, and *H. bivittatus* juveniles and IP adults were all negatively associated with adult beaugregory damselfish. Juvenile yellowtail damselfish also appear to be strongly negatively correlated with all of the labrid species and their life stages. *Halichoeres garnoti* juveniles and TP adults are strongly associated with algae on sand. Interestingly, despite variability in depth and topographic complexity among the

back reef sites, labrid species do not appear to be greatly affected by these factors.

For the back reef data set with damselfish excluded, 17.6% of the variation in labrid variables was explained by the environmental variables, and the eigenvalues for Root 1 and 2 were lower than in the analysis with damselfish included (Table 7.4). From the ordination plot, microhabitat associations are more clearly explained (Fig. 7.15). Furthermore, variation in depth and topographic complexity are non-significant for the labrid life stages and species that feature prominently in the back reef zone. *Halichoeres bivittatus* IP adults are strongly associated with algae on sand, and *H. bivittatus* juveniles and *H. garnoti* TP adults are strongly associated with sand. *Halichoeres maculipinna* juveniles and *H. poeyi* IP adults both appear to be more strongly associated with live *Montastrea annularis* and other live corals than other microhabitats.

For the fore reef data set, with all environmental variables included in the model, the percentage of variance in labrid variables explained by environmental variables is only 13.5%, compared with 21.8% for the back reef data set (Table 7.4). From the ordination plot, the biological associations were not as interpretable as those from the ordination plots of the back reef data set (Fig. 7.16). One strong negative association is between *Thalassoma bifasciatum* IP adults and pavement microhabitats. *Halichoeres maculipinna* juveniles and *H. garnoti* TP adults are also negatively associated with pavement. *Halichoeres garnoti* juveniles and *H. garnoti* IP adults are closely associated with adult bicolor damselfish.

For the fore reef data set with damselfish excluded from the environmental variables, a relatively smaller percentage of variation in labrid variables was accounted for by environmental variables compared with the other analyses (Table 7.4). From the ordination plot, *H. maculipinna* juveniles and *T. bifasciatum* IP adults are both negatively associated with *P. porites* rubble, live *P. porites*, and pavement microhabitats. *Halichoeres maculipinna* TP adults are closely associated with pavement microhabitats, and *H. garnoti* IP adults are closely associated with sand.

DISCUSSION

Along with the geographical separation of fore reef and back reef sites, zonation is apparently a primary explanation for the spatial patterns in wrasse assemblage structure. There are high abundances of *H. bivittatus* and *H. poeyi* on the back reef, compared with low abundances at fore reef locations. *Thalassoma bifasciatum* dominates the fore reef sites, which further distinguishes fore reef labrid assemblages from back reef labrid assemblages. *Halichoeres maculipinna*, and *H. garnoti* do not show extremely large differences in abundance between fore reef and back reef sites. *Halichoeres radiatus* was the rarest labrid included in this study. Within each species, there were apparent variations in the level of recruitment and population sizes between 1997 and 1998. Within a year, levels of recruitment and population sizes were not consistent across sites. These patterns could be the result of 1) differential availability of larvae, 2) patterns of settlement and habitat selection by postlarvae (settlers), and/or 3) differential survivorship after settlement.

Caselle and Warner (1996) recently tested the hypothesis that habitat features are more likely to influence recruitment patterns of *Thalassoma bifasciatum* at a smaller spatial scale (transects within sites) than at a larger scale (sites around St. Croix, U.S.V.I.). They found that at the small scale, certain features of the habitat significantly predicted recruitment density. None of the microhabitat features that predicted recruitment at the small scale could predict the patterns at the large scale. Instead, physical oceanographic processes appeared to be responsible for patterns of recruitment. Although Caselle and Warner (1996) found consistent patterns of recruitment to sites, they did not find habitat selection an important factor at the site scale. However, once delivered to a site, settlers or new recruits distributed themselves based on microhabitat preferences. In the present study, if oceanographic processes are the primary factor responsible for delivery of recruits to a site, then why the discrepancy among species with respect to the levels of

recruitment across sites? For example, high levels of recruits were censused at Cane Bay for both *Halichoeres garnoti* and *Thalassoma bifasciatum*, but very few recruits of *H. bivittatus* and *H. poeyi* were observed at this site. It is doubtful that recruits of the latter two species arrive at Cane Bay and simply experience very high rates of mortality. More likely, it is the combination of oceanographic processes and selection by larvae for particular large scale reef characteristics that differentiate one reef zone from another. Clearly, delivery of larvae (passively or actively), is not occurring at the same rates among reef sites around St. Croix for different labrid species.

Long-term studies on communities of fishes on both temperate and coral reefs have demonstrated that the quantitative and qualitative composition of their constituent species varies significantly, both spatially and temporally (e.g. Stephens and Zerba 1981, Choat et al. 1988, Carr 1989, Sale et al. 1994, Holbrook et al. 1994, Ault and Johnson 1998). In the present short-term study, it was found that numbers of labrid adults on reefs of St. Croix do not remain constant, instead, they fluctuate from year to year. Some species show greater population fluctuations than others. In a separate study on labrids of the Great Barrier Reef, Eckert (1987) found large differences in survival for newly settled labrids (ranging from 75% to 8.2%). Consequently, she found that the rank order of abundances of juveniles that survived the first twelve months was very different from the rank order of the number of recruits settling to the reefs. She found that time is a significant predictor of mortality (logically), but different species suffer different mortality rates. This is likely the case in Caribbean labrids as well.

Zonation was also an apparent factor in affecting the abundance of damselfish species at the different study sites. Bicolor and threespot damselfish were most common on fore reef sites. Dusky were present in high numbers in both reef zones, but they were more abundant on the fore reef sites. Beaugregory damselfish were most common on the back reef sites. At several sites, uni-specific colonies of adult damselfish were observed similar to those described by Itzkowitz

(1977b). He suggested that the eventual formation of uni-specific adult colonies is due to 1) differential mortality of the juveniles (probably selective predation) 2) substratum preferences of the adults, and 3) a behavioural system which inhibits other species from sharing a common territorial border on a homogeneous substratum.

From the CCA, negative associations were apparent between adult beaugregory damselfish and *H. maculipinnna* juveniles, *H. poeyi* juveniles and IP adults, and *H. bivittatus* juveniles and IP adults on the back reef sites. It was found in Chapters III, IV, and VI that interactions with damselfish may be important to the spatial arrangements and movements of these labrids. First, time budget analyses of behaviour indicated that approximately 5% of behaviours recorded involved agonistic interactions with territorial damselfish (Chapter III). Second, an investigation into the distribution of behaviours throughout individual home ranges indicated a significant portion of agonistic encounters with damselfish was occurring in the peripheries of labrid home ranges (Chapter IV). Third, experimental introductions of adult beaugregory damselfish into the center of adult *Halichoeres bivittatus* home ranges, and adjacent to juvenile *H. bivittatus* home ranges, caused a significant increase in beaugregory- *H. bivittatus* interactions (Chapter VI). This resulted in a significant reduction in the amount of time adult slippery dicks could spend foraging or in a foraging assemblage. Overall, results of that experiment suggest that aggressive interactions with territorial pomacentrids affect individual space use in *Halichoeres bivittatus*. The present study confirmed the hypothesis that adult beaugregories affect spatial distribution of some *Halichoeres* species and their life stages on the spatial scale or ecological level beyond that of individual home range. The hypothesis was not supported for damselfish other than beaugregories, and needs to be further investigated on reefs in other locales where different environmental parameters and population densities are present. Furthermore, CCA examines correlations and one cannot infer causation from the correlations.

One additional aspect to this study was to investigate the associations between labrids, depth, topographic complexity, and microhabitat availability. Interestingly, despite variability in depth and topographic complexity among the sites within a zone, labrid species do not appear to be greatly affected by these factors at this spatial scale. On smaller spatial scales, topographic complexity may be more important to some of the labrid species and their life stages than others. For example in Chapter V, it was found that as these labrids grow, they increase their use of topographically simple microhabitats. The CCA also revealed associations between some labrids and certain microhabitats. In Chapter V, it was found through observations of focal fish that several species showed preferences for particular microhabitats, such as *Halichoeres bivittatus* and sand microhabitats, and *H. poeyi* and algae on coral rubble. To answer the question posed earlier “Do these preferences for small patches within their home range areas result in detectable associations between species abundances and microhabitat availability on larger spatial scales?": in some cases yes, but not all. The different labrid species require similar amounts of space per body length (Chapter II), so generalities about why some small scale associations between labrids and microhabitats are observable patterns in population distributions and others are not, would be difficult to explain.

The CCA also revealed differences among life stages within a species and associations with microhabitats. This supports the suggestion in Chapter V that ontogenetic shifts in microhabitat use in these labrids may sometimes be larger than differences in microhabitat use for heterospecifics of the same life stage.

Concluding statements

This study investigated environmental factors that affect the patterns of distribution for Caribbean labrid species. Zonation was clearly important in labrid assemblage structure due to the absence of *Halichoeres bivittatus* and *H. poeyi* and the dominance of *Thalassoma bifasciatum* on

fore reef sites. Depth within zones and topographic complexity were not strongly associated with labrid abundances. Within zones, however, several associations between labrids and microhabitats and a negative association between some labrids and adult beaugregories were revealed.

Underlying mechanisms on smaller spatial scales (i.e. that of individual home range use, social interactions, and microhabitat selectivity) were discussed as possible influences on the patterns observed and the correlations revealed through CCA.

Table 7.1. Summary of the sampling design of visual censuses combined for 1997 and 1998. Listed are the numbers of censuses per site and whether or not the environmental parameters were quantified.

Zone	Site	# Transects	# Labrid Censuses	# Damselfish Censuses	Microhabitat Quantification?	Complexity?	Depth?
FORE	Cane Bay	6	5	3	yes	no	yes
	Tague Bay (TB)1	8	24	10	yes	yes	yes
	TB 2	8	24	10	yes	yes	yes
	TB 3	8	24	12	yes	yes	yes
BACK	TB 4	8	24	10	yes	yes	yes
	TB 5	8	24	10	yes	yes	yes
	TB 6	8	24	10	yes	yes	yes
	South Shore	6	3	2	yes	no	no

Table 7.2. A list of the pomacentrids included in the visual censuses. Information is taken from Bohlke and Chaplin (1968) and Allen (1991).

Common Name	Species Name	Authority	Maximum Total Length (cm)	Depth Range (m)
Beaugregory	<i>Stegastes leucostictus</i>	Müller and Troschel	9	0-5
Bicolor	<i>S. partitus</i>	Poeyi	12	0-45
Cocoa	<i>S. variabilis</i>	Castelnau	11	0-30
Dusky	<i>S. dorsopunicans</i>	Poeyi	13	0-3
Longfin	<i>S. diencaeus</i>	Jordan and Rutter	11	2-5
Threespot	<i>S. planifrons</i>	Cuvier	12	1-30
Yellowtail	<i>Microspathodon chrysurus</i>	Cuvier	21	0-10

Table 7.3. Average depth and degree of topographic complexity at the study sites. See methods for explanations of how these measures were quantified. The averages are followed by the standard error in parentheses. (n.a. = not measured)

ZONE	SITE	DEPTH (m)	DEGREE OF TOPOGRAPHIC COMPLEXITY
FORE	Cane Bay	7.0 (0.1)	n.a.
	Tague Bay Site 1 (TB1)	5.8 (0.1)	7.4 (0.6)
	TB2	6.7 (0.1)	8.2 (0.6)
	TB3	5.0 (0.1)	9.3 (0.8)
BACK	TB4	1.6 (0.1)	5.0 (0.7)
	TB5	1.6 (0.1)	4.9 (0.6)
	TB6	1.3 (0.1)	8.6 (1.1)
	South Shore	n.a.	n.a.

Table 7.4. Percentage of variance extracted and redundancy of labrid and environmental data sets for the first two canonical factors. The back reef sites and fore reef sites were analysed separately either with or without damselfish included as environmental variables.

REEF ZONE	Data Set	CCA Root	Eigen-value	Labrid Data: % Variance Extracted	Labrid Data: % Redundancy	Environmental Data: % Variance Extracted	Environmental Data: % Redundancy	% Labrid Variance explained ¹
BACK	with damselfish $R^2 = 0.862$	1	0.744	11.3	8.4	9.6	7.1	21.8
		2	0.449	8.9	4.0	10.9	4.9	
	without damselfish $R = 0.611$	1	0.373	9.1	3.4	15.8	5.9	17.6
		2	0.352	7.7	2.7	12.0	4.2	
FORE	with damselfish $R = 0.677$	1	0.458	10.4	4.8	7.6	3.5	13.5
		2	0.444	7.1	3.1	7.5	3.3	
	without damselfish $R = 0.535$	1	0.286	8.4	2.4	13.7	3.9	11.6
		2	0.224	7.0	1.6	8.6	1.9	

¹Equals the % of labrid variance explained by environmental variables.

²R = Canonical R

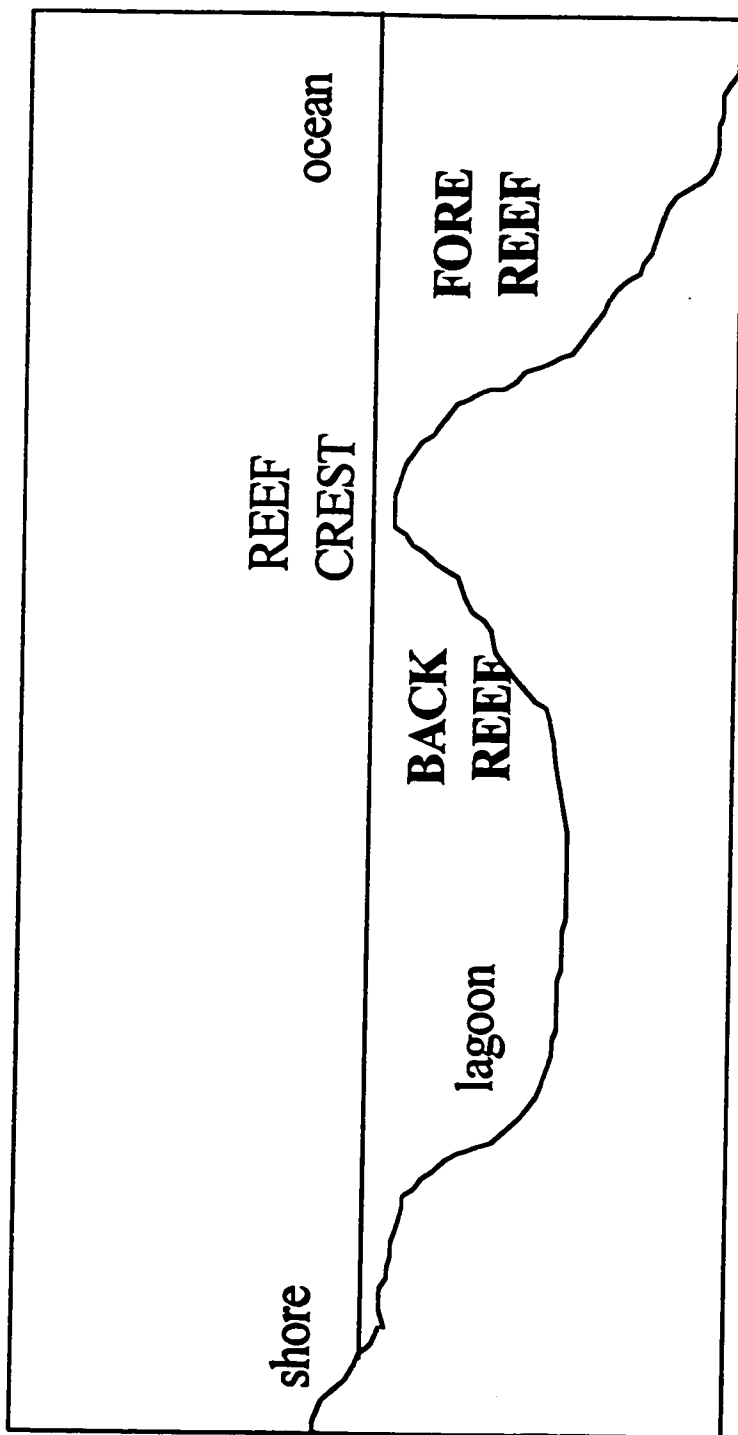


Fig. 7.1. Diagram of back reef and fore reef zones.

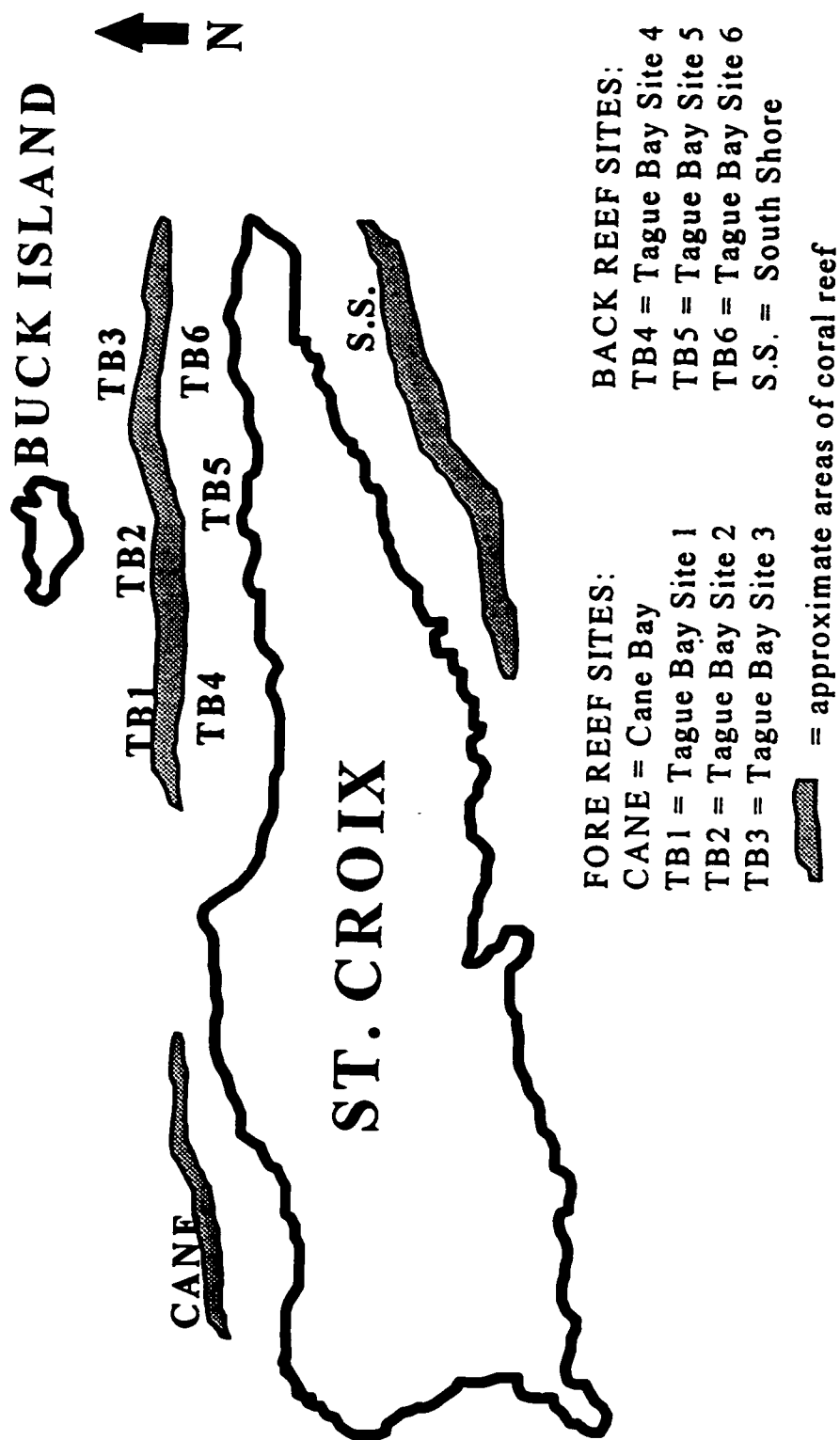


Fig. 7.2. Map of St. Croix, U.S.V.I. showing the approximate locations of sampling sites.

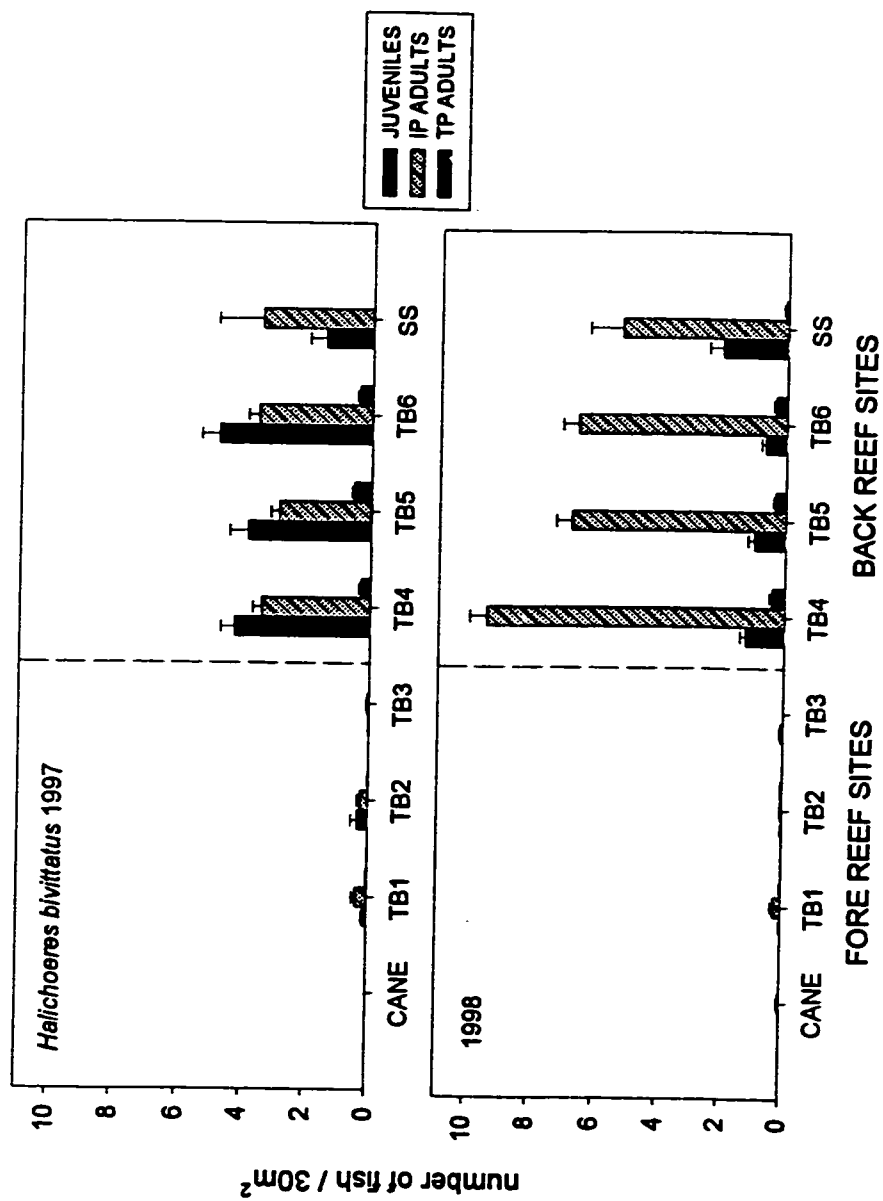


Fig. 7.3. Relative abundances of the three life stages of *H. bivittatus* at the eight sampling sites around St. Croix. The averages are fish counts per transect (+ 1 s.e.) and are obtained from pooling the census dates within each year. The site codes correspond to the map labels in Fig. 7.2.

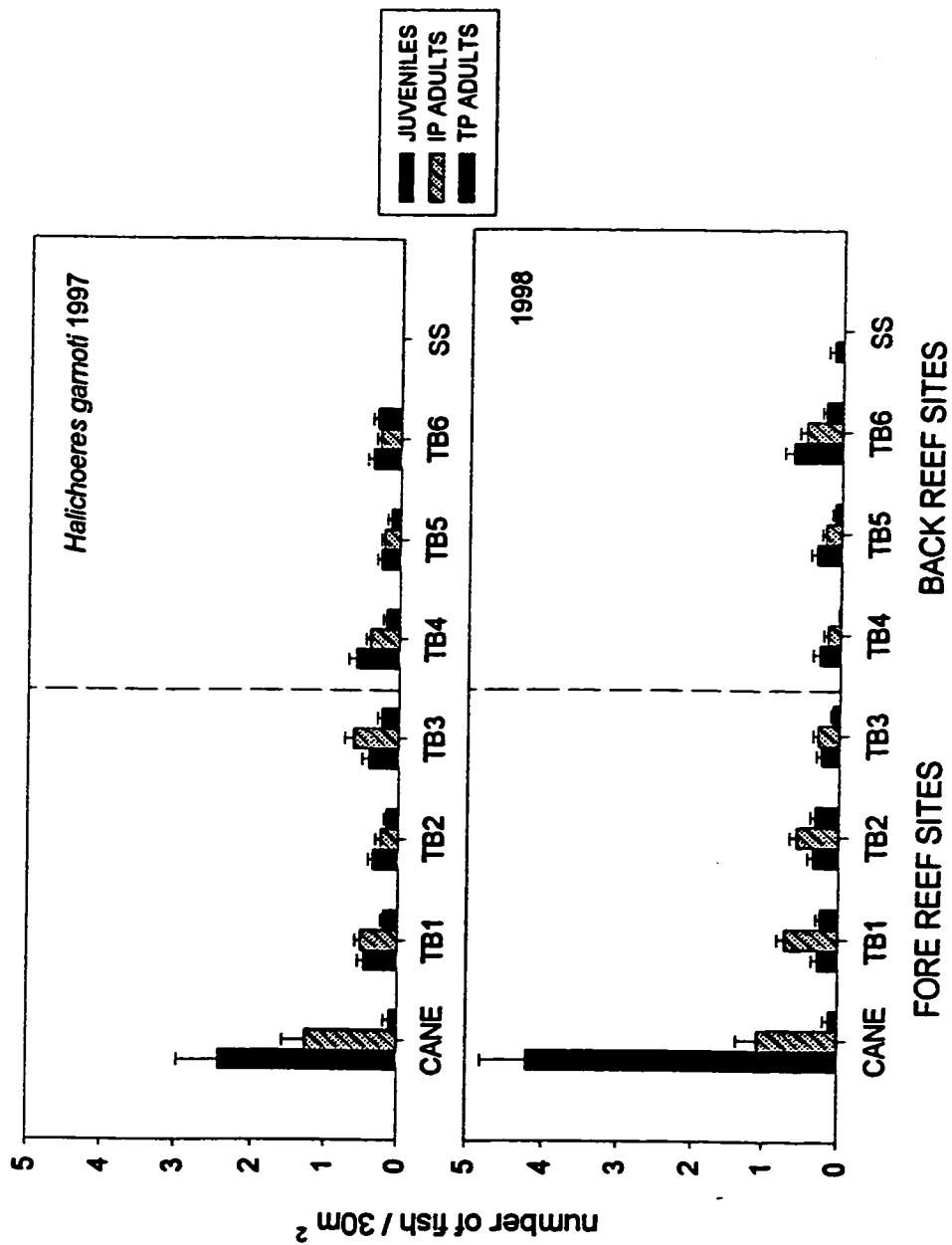


Fig. 7.4. Relative abundances of *H. garnoti* at the sampling sites around St. Croix. The explanation is the same as for Fig. 7.3.

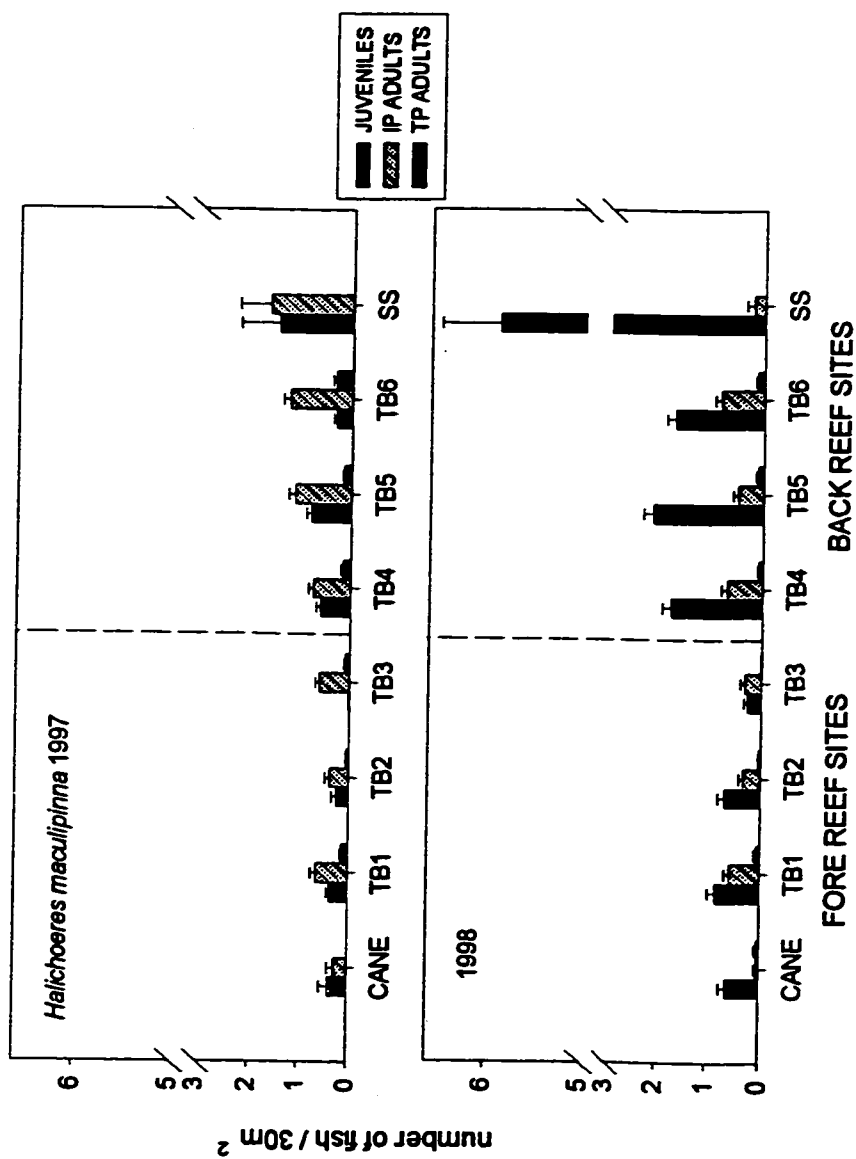


Fig. 7.5 Relative abundances of *H. maculipinna* at the sampling sites around St. Croix. The explanation is the same as for Fig. 7.3.

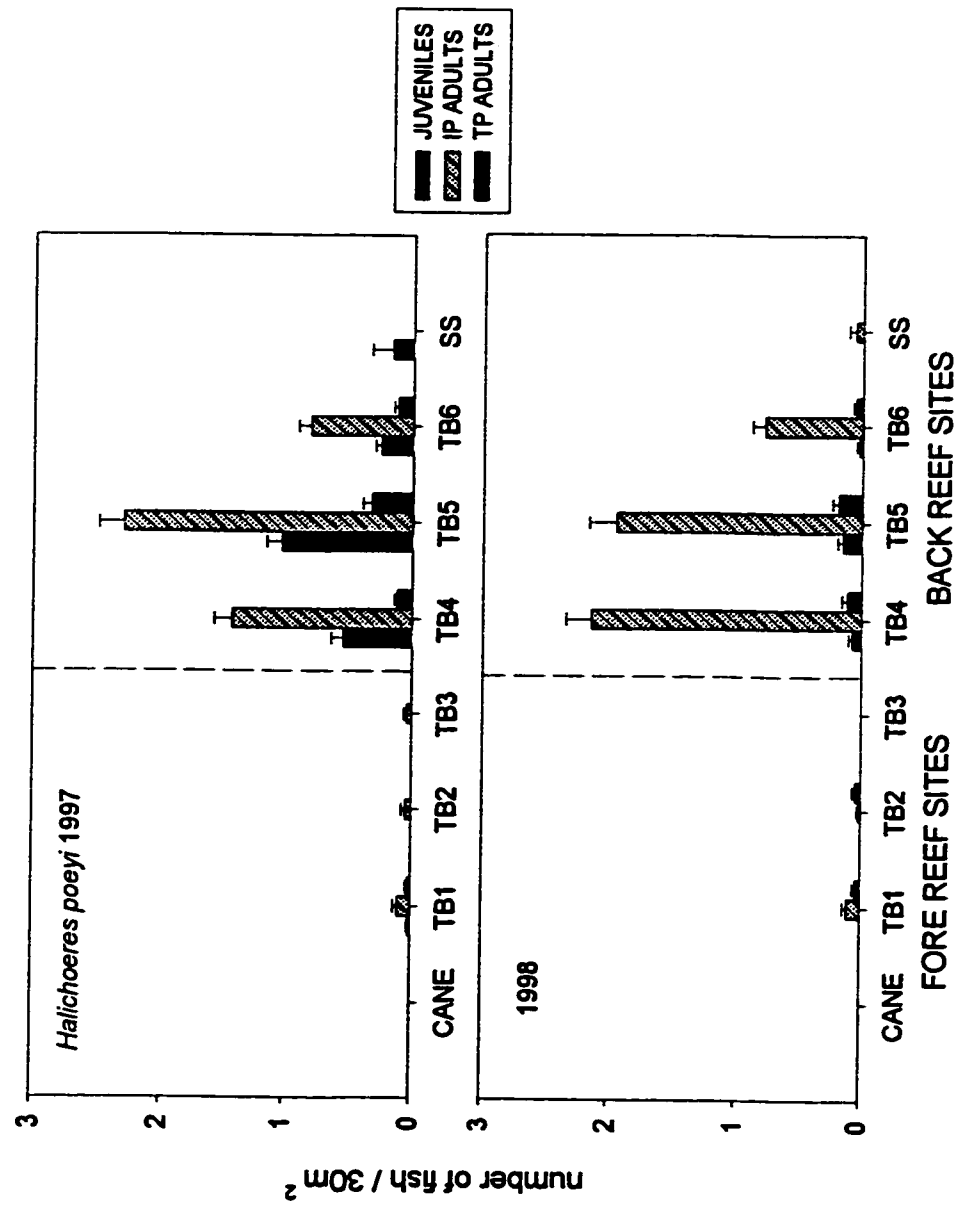


Fig. 7.6. Relative abundances of *H. poeyi* at the sampling sites around St. Croix. The explanation is the same as for Fig. 7.3.

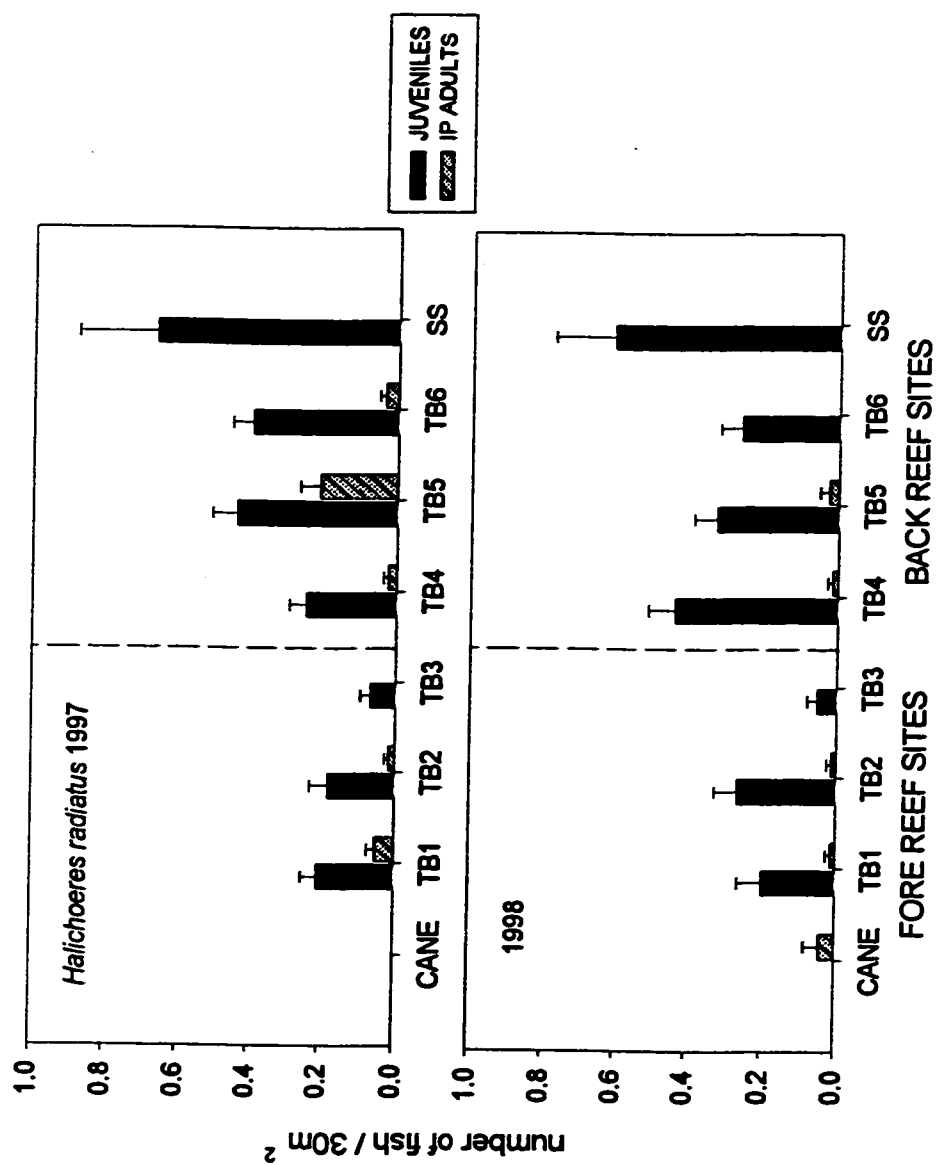


Fig. 7.7. Relative abundances of juvenile and adult *H. radiatus* at the sampling sites around St. Croix. The explanation is the same as for Fig. 7.3.

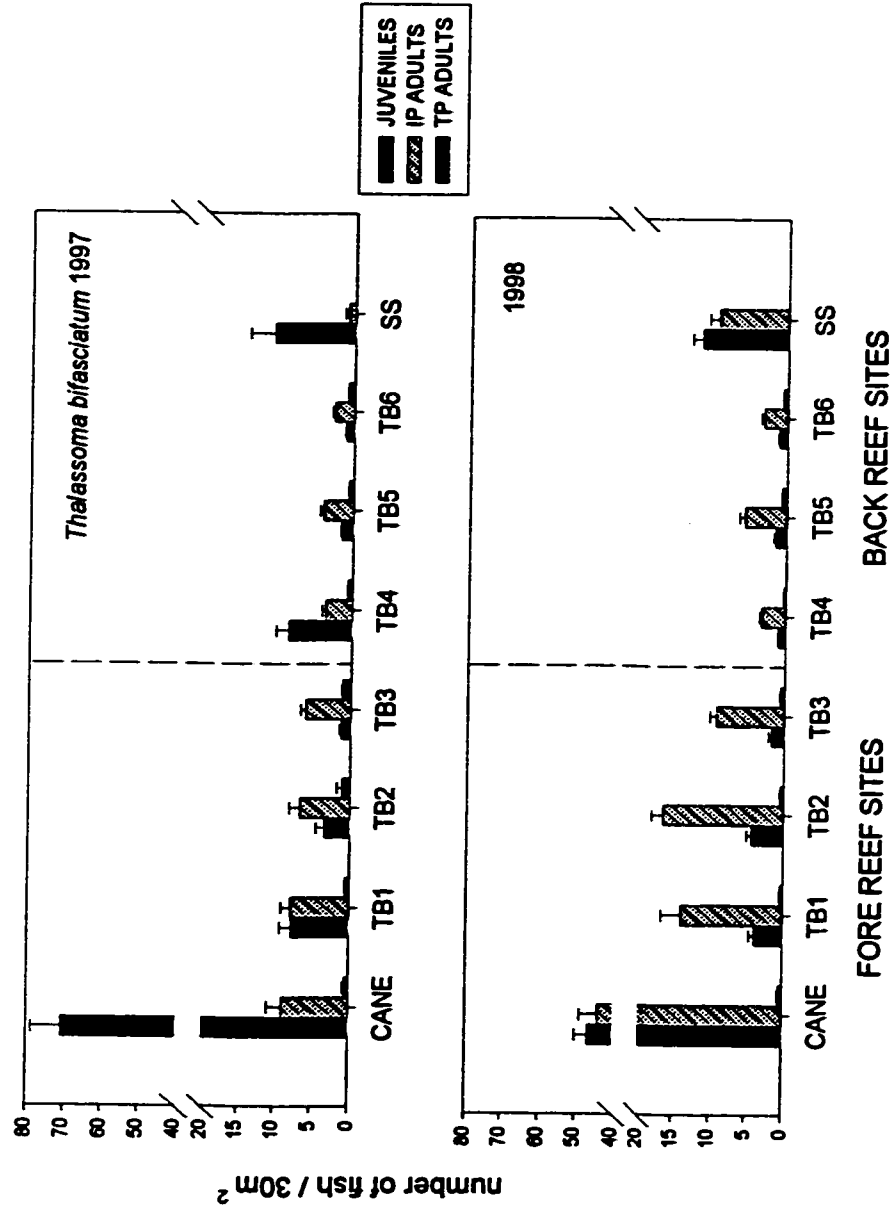


Fig. 7.8. Relative abundances of the three life stages of *Thalassoma bifasciatum* at the sampling sites around St. Croix. The explanation is the same as for Fig. 7.3.

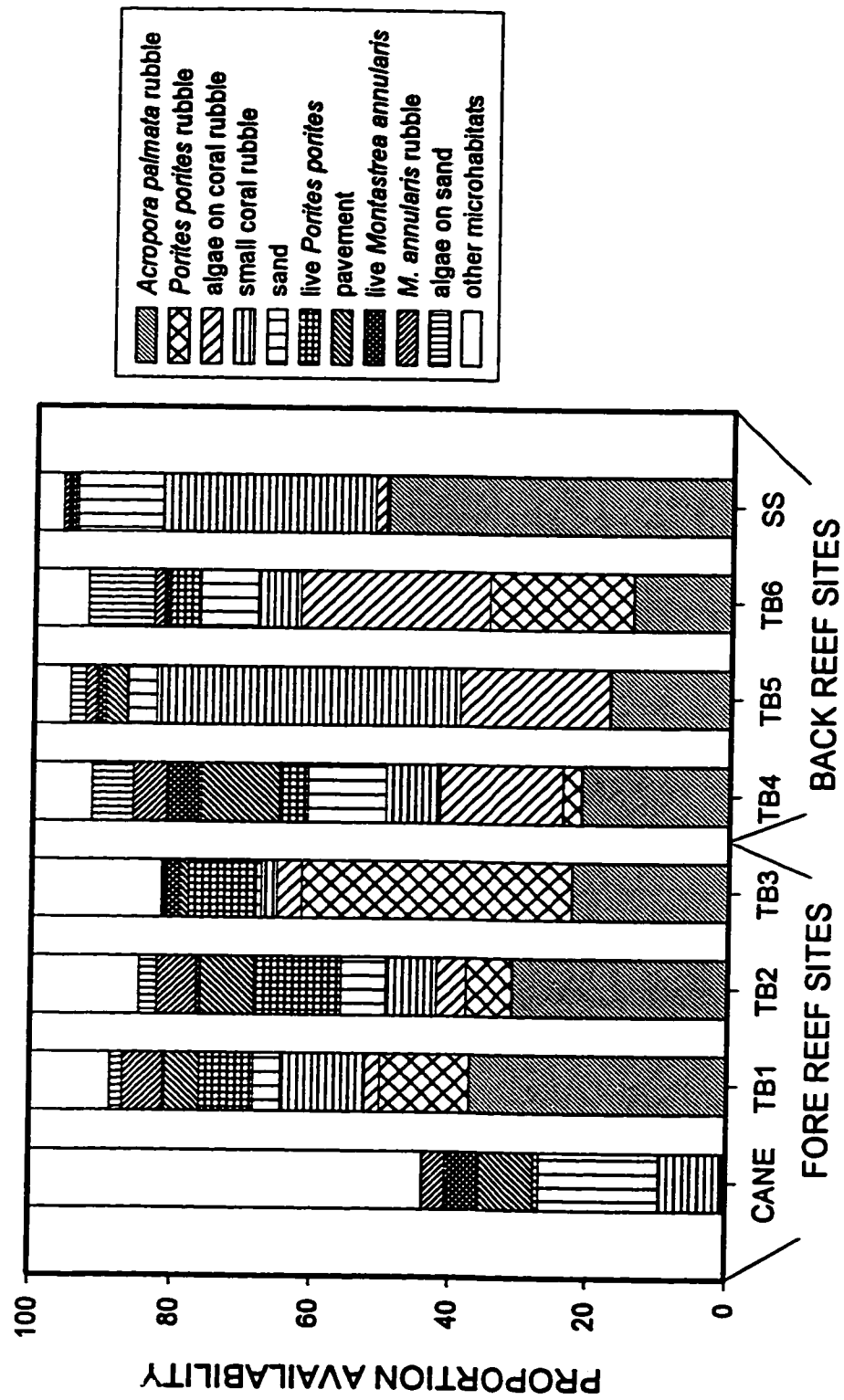


Fig. 7.9. Proportion availability of microhabitats at the eight sampling locations around St. Croix.

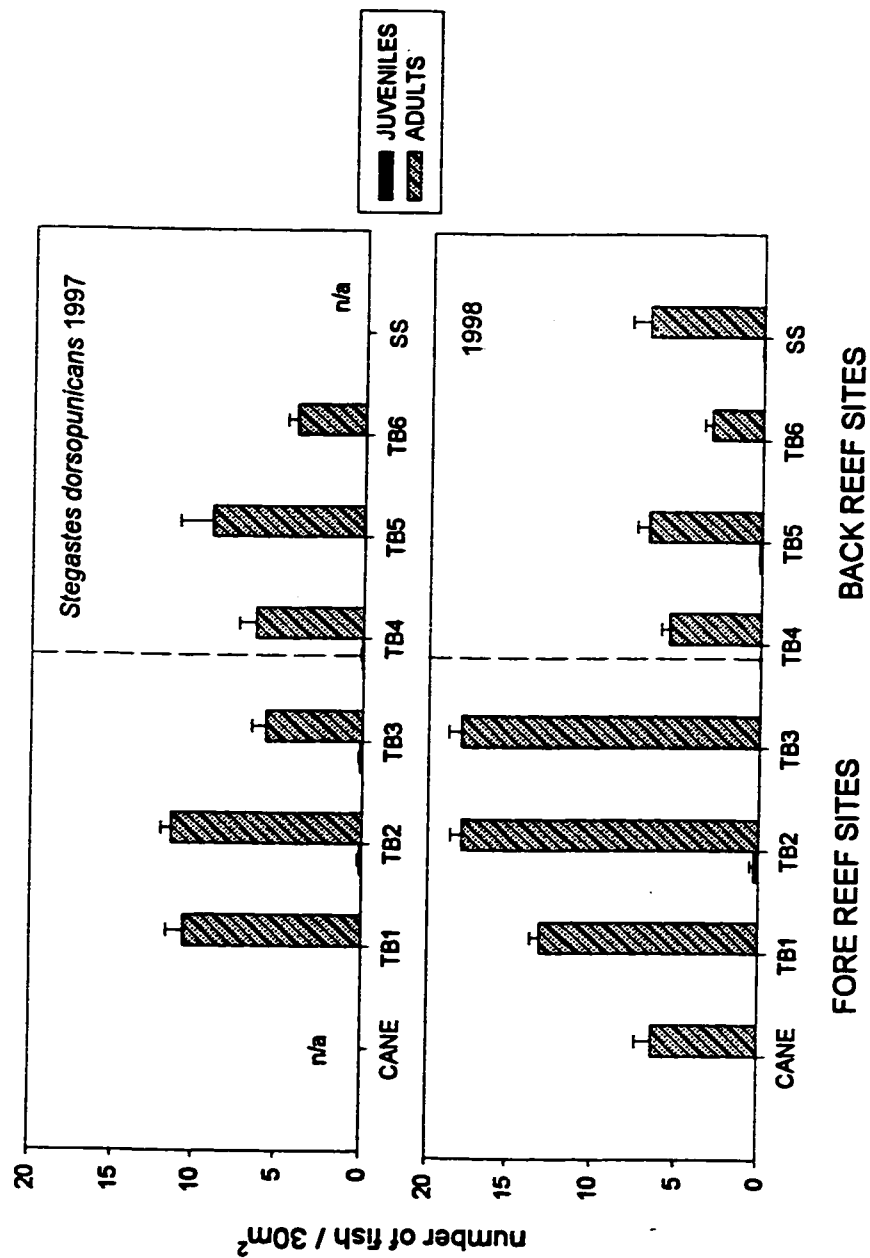


Fig. 7.10. Relative abundances of the dusky damselfish, *S. dorsopunicans*, at the eight sampling sites around St. Croix. The averages are fish counts per transect (+ 1 s.e.) and are obtained from pooling the census dates within each year. The site codes correspond to the map labels in Fig. 7.2.

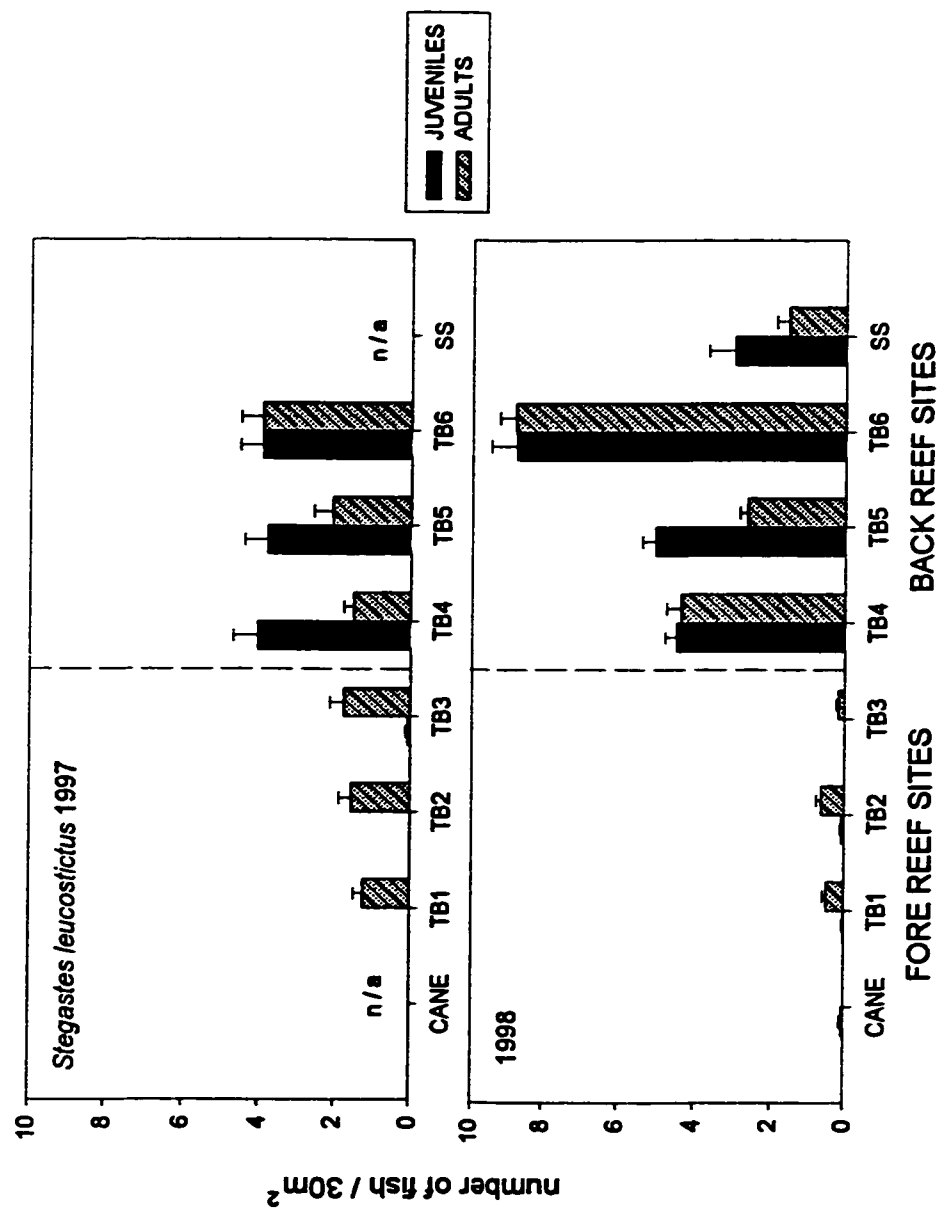


Fig. 7.11. Relative abundances of the beaugregory damselfish, *S. leucostictus*, at the eight sampling sites around St. Croix. The explanation is the same as for Fig. 7.10.

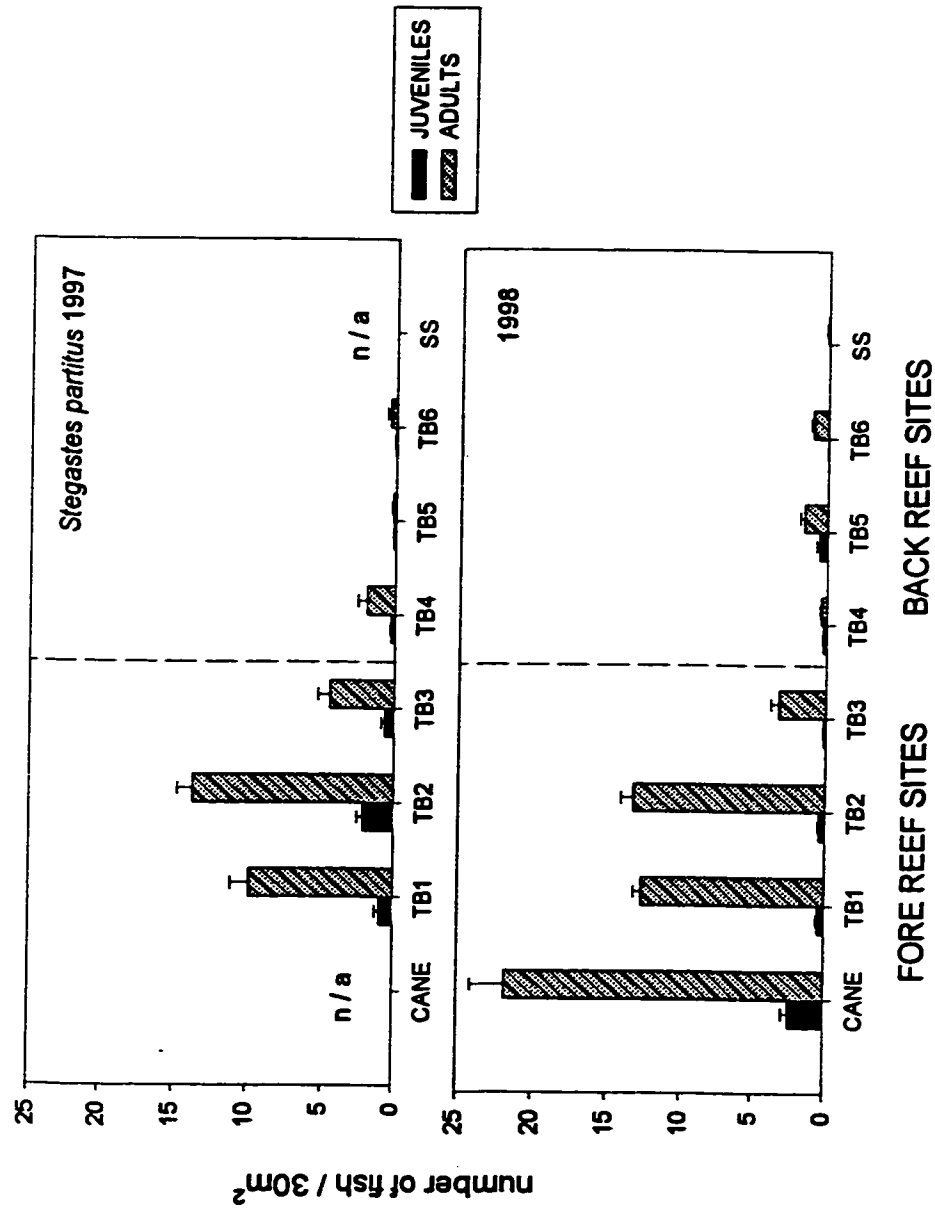


Fig. 7.12. Relative abundances of the bicolor damselfish, *S. partitus*, at the eight sampling sites around St. Croix. The explanation is the same as for Fig. 7.10.

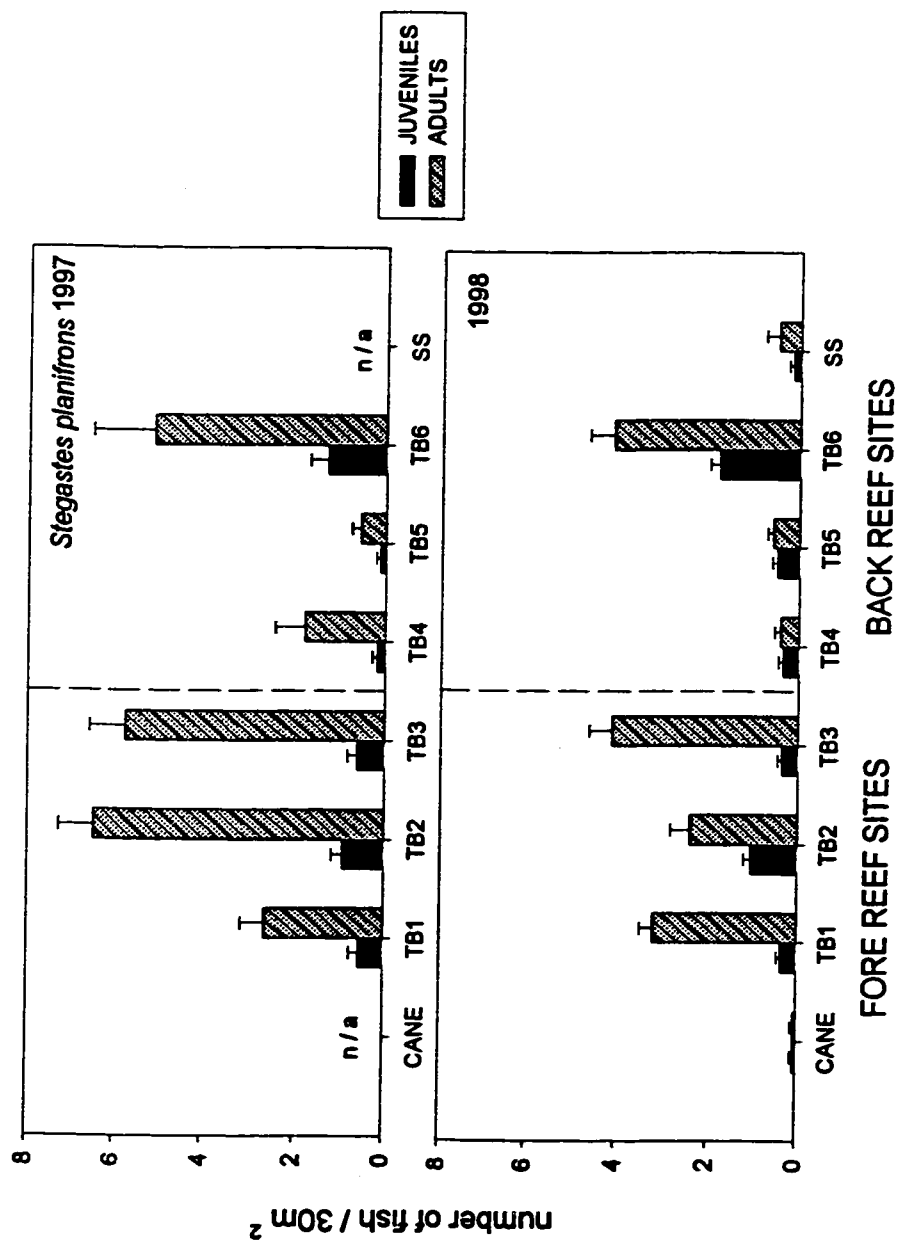


Fig. 7.13. Relative abundances of the three spot damselfish, *S. planifrons*, at the eight sampling sites around St. Croix. The explanation is the same as for Fig. 7.10.

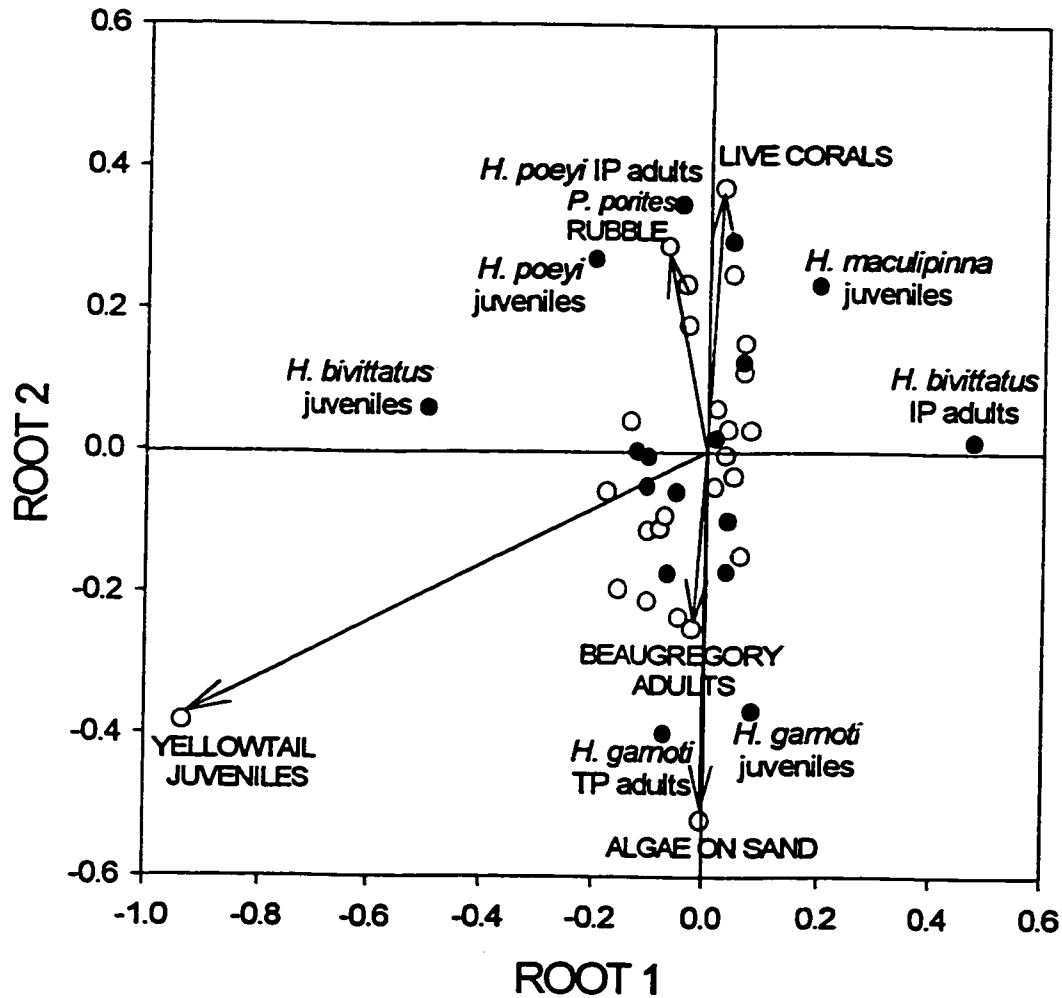


Fig. 7.14. Ordination plot of the first two roots of CCA of environmental variables (including damselfish abundances) and labrid variables from back reef sites. Environmental variables are represented by open circles and are capitalized (except coral species names), and labrid variables are represented by black circles, and are italicized (except life stages). Only those microhabitat variables that had factor loadings greater than $|0.3|$ are indicated with vector arrows and labels, and only species names that show strong correlations with either root (i.e. factor loadings greater than $|0.25|$) are labelled (for visual clarity).

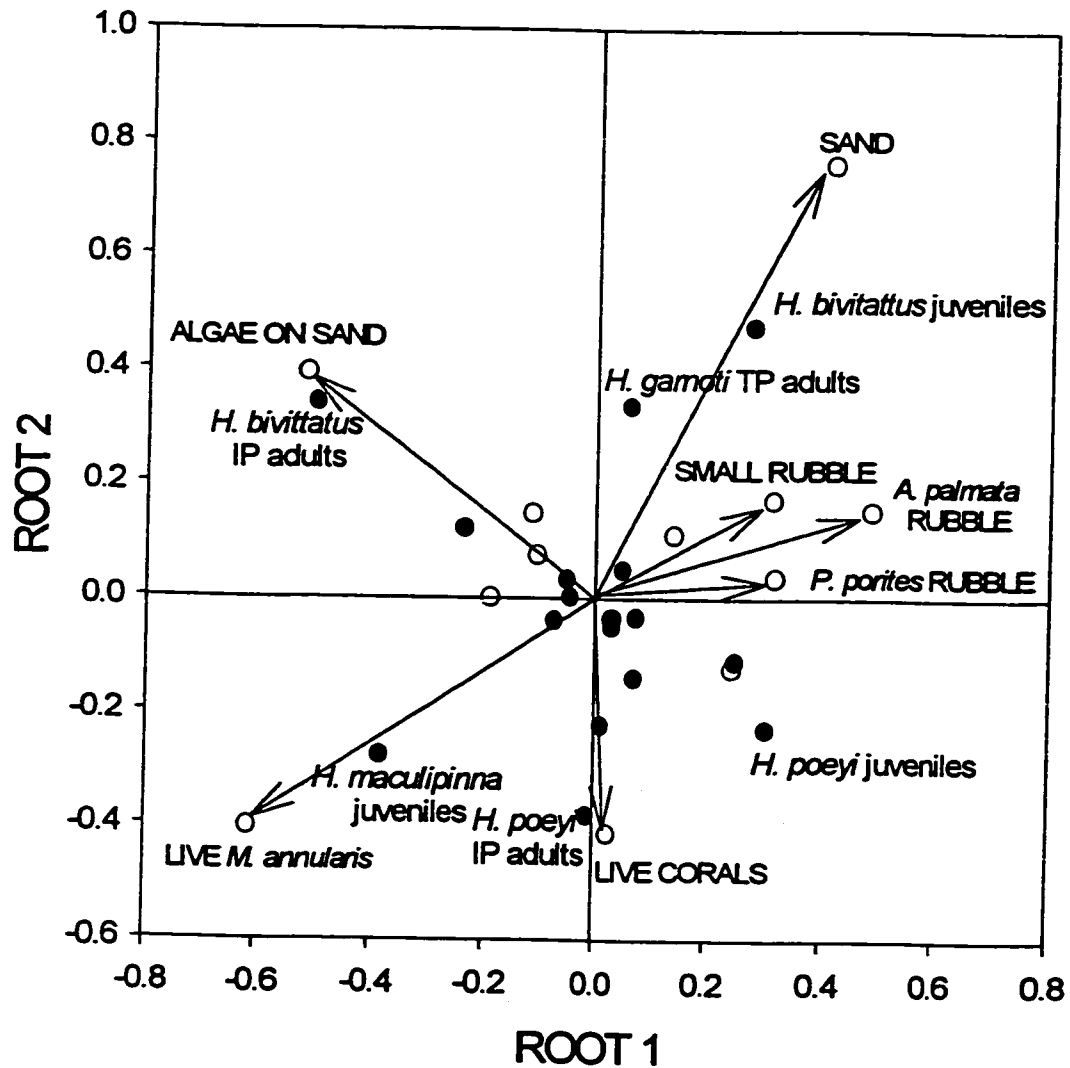


Fig. 7.15. Ordination plot of the first two roots of CCA of environmental variables (excluding damselfish abundances) and labrid variables from back reef sites. Environmental variables are represented by open circles and are capitalized (except coral species names), and labrid variables are represented by black circles, and are italicized (except life stages). Only those microhabitat variables that had factor loadings greater than $|0.3|$ are indicated with vector arrows and labels, and only species names that show strong correlations with either root (i.e. factor loadings greater than $|0.25|$) are labelled (for visual clarity).

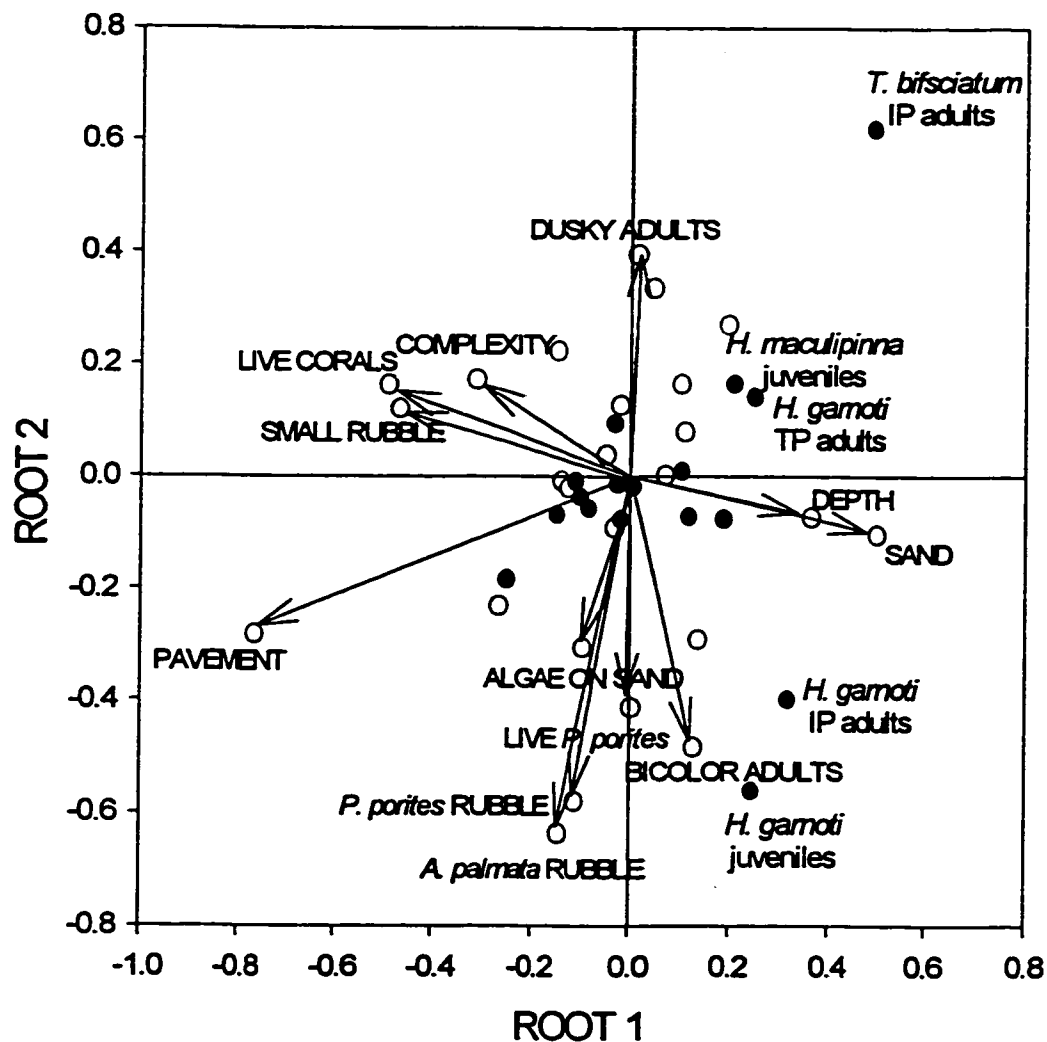


Fig. 7.16. Ordination plot of the first two roots of CCA of environmental variables (including damselfish abundances) and labrid variables from fore reef sites. Environmental variables are represented by open circles and are capitalized (except coral species names), and labrid variables are represented by black circles, and are italicized (except life stages). Only those microhabitat variables that had factor loadings greater than $|0.3|$ are indicated with vector arrows and labels, and only species names that show strong correlations with either root (i.e. factor loadings greater than $|0.25|$) are labelled (for visual clarity).

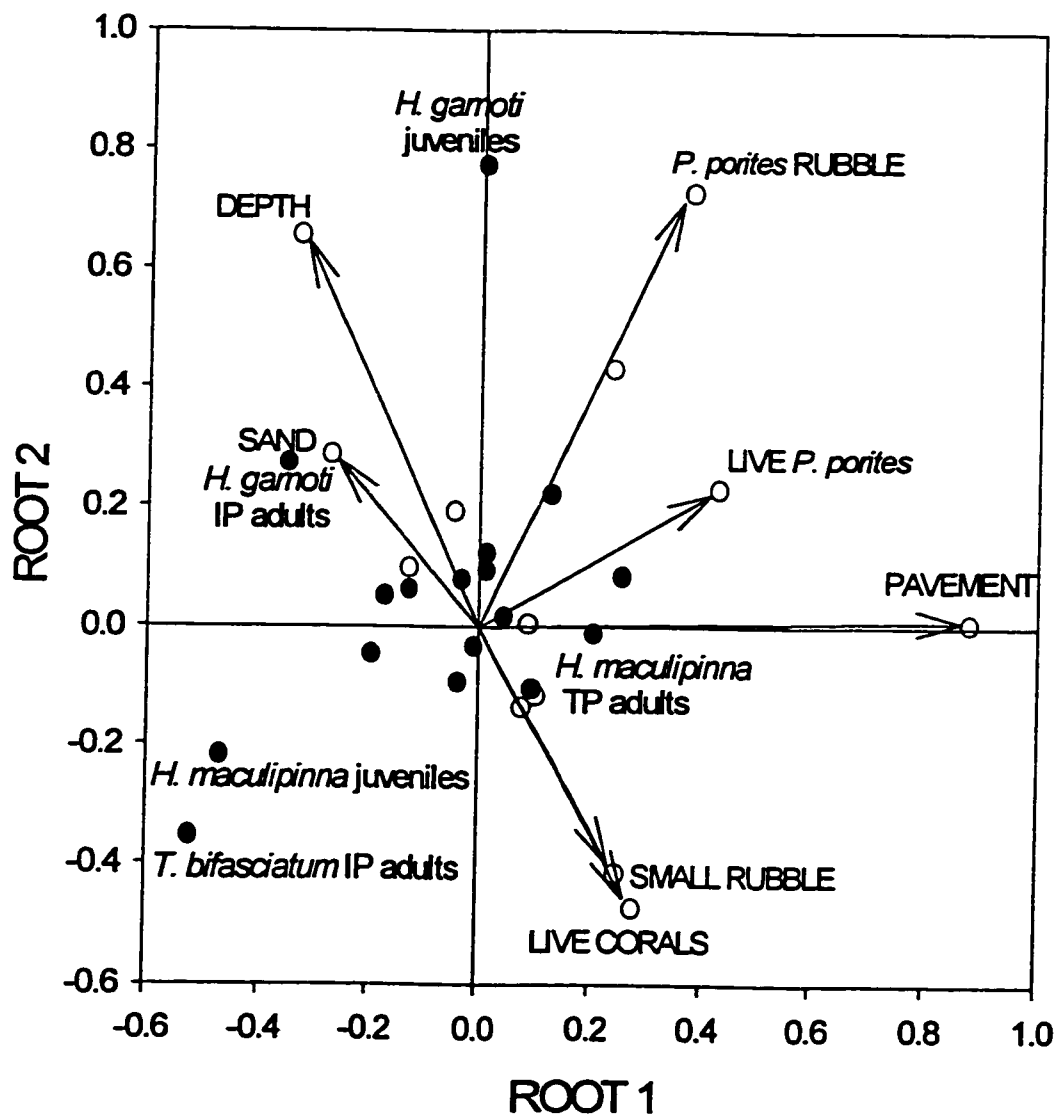


Fig. 7.17. Ordination plot of the first two roots of CCA of environmental variables (excluding damselfish abundances) and labrid variables from fore reef sites. Environmental variables are represented by open circles and are capitalized (except coral species names), and labrid variables are represented by black circles, and are italicized (except life stages). Only those microhabitat variables that had factor loadings greater than $|0.3|$ are indicated with vector arrows and labels, and only species names that show strong correlations with either root (i.e. factor loadings greater than $|0.25|$) are labelled (for visual clarity).

CHAPTER VIII

GENERAL DISCUSSION

This dissertation investigated many aspects of spatial dynamics, behaviour, social interactions, and microhabitat use in ecologically similar labrid species. The purpose of this general discussion is to integrate the main findings from each chapter. The main points from the chapters can be collectively grouped into categories, namely: 1) factors affecting home range size and arrangement, 2) factors affecting the establishment of activity centers within home range areas, 3) high degrees of ontogenetic and heterospecific overlap in microhabitat use and behaviour, 4) factors that potentially promote coexistence, 5) effects of territorial pomacentrids on labrids, and 6) local mechanisms that generate patterns in assemblage structure on larger spatial scales.

Factors affecting home range size and arrangement

The labrids investigated all had significant positive relationships between \log_{10} home range area, and \log_{10} fish total length (Chapter II). The rates of increase were very similar among the species. After pooling three of the species that did not differ significantly in the relationship between home range area and fish length (*Halichoeres bivittatus*, *H. garnoti*, and *Thalassoma bifasciatum*), it was observed that once individuals reach the initial phase, home range area reaches a plateau.

What factors may affect home range area requirements? Three possible factors include: 1) resource requirements (food or microhabitat), 2) “social facilitation”, whereby the focal fish expands its home range boundary until a minimum number of social contacts are established (e.g. Norman and Jones 1984), or 3) “social inhibition”, whereby the focal fish contracts its home range

to reduce or minimize the negative or costly interactions with neighbouring competitors.

Resource requirements may play a large role in determining home range size in these labrids. In explaining why a species occupies a feeding territory of a certain size, optimal foraging theory is often invoked (Gerking 1994). Such an explanation hypothesizes that food density and territory size are inversely related. In the case of the labrids in this study, the resource may be microhabitat availability, microhabitat diversity, or food requirements. Experimental investigations (e.g. food supplementation or microhabitat manipulations) would elucidate the effects of these resources on home range area.

The “social facilitation” hypothesis predicts that in locations of lower labrid densities (with equivalent resource densities as areas with higher labrid densities), home range areas would be larger. In a study with a temperate territorial damselfish, *Parma victoriae*, Norman and Jones (1984) obtained results that suggest individuals of this species may increase their home range movements until touching other territories in order to maintain social contact with members of the opposite sex (or, in the case of labrids, any individual that provides a foraging partnership). Observational studies combined with transplant experiments could test this hypothesis.

“Social inhibition” of labrid home range size could result from competitive interactions with other labrids, or territorial pomacentrids. For example, in a study on home range area in temperate labrids (*Pseudolabrus* species), Matsumoto et al. (1999) found that agonistic interactions between similar-sized individuals, irrespective of species, restricted the home range size of these labrids. However, for the labrid species in the present study, agonistic encounters were minimal between conspecifics, both within and between size classes (discussed in Chapter III). Therefore, social inhibition by conspecific or heterospecific labrids did not affect home range size in these labrids. Additionally, social inhibition by territorial damselfish did not affect home range size in these labrids. This was investigated in Chapter VI through a field experiment that

introduced the territorial beaugregory damselfish into the activity centers of adult *Halichoeres bivittatus* home ranges and adjacent to juvenile *H. bivittatus* home ranges. The results of this experiment suggested that beaugregories have no effect on home range area of *H. bivittatus*.

Although the introduction of beaugregories did not affect home range areas in *H. bivittatus*, it did force home range relocations (Chapter VI). These results suggested that for *H. bivittatus*, home range shape is much more flexible than home range area. The fluidity of home range boundaries has recently been considered by other researchers (Eifler 1996, Frederick 1997, Gordon 1997). Animals commonly reposition their activity areas, making better use of resource availability (Eifler 1996). Gordon (1997) stated that home ranges are not fixed parcels of real estate, and described home range dynamics as ‘continual adjustments of shared boundaries’: “every individual has a unique configuration of neighbors, and if each individual affects its neighbors’ growth and survival, then the conditions at each site are perpetually changing the conditions nearby”.

Factors affecting the establishment of activity centers within home range areas

The presence of activity centers within home range areas was also investigated. It was found that 50% core use areas (defined as containing 50% of the observation points) encompassed only 13-26% of the home range area (Chapter II), and 30% core use areas encompassed only 8 to 16% of the home range area (Chapter IV). What determines the positioning of core use areas? In Chapter IV, it was observed that some behaviours were randomly distributed throughout home range areas, whereas others were non-randomly distributed. The most significant and consistent finding was the non-random distribution of agonistic interactions with territorial pomacentrids throughout home ranges for *H. bivittatus*, *H. garnoti*, *H. poeyi*, *H. radiatus*, and *Thalassoma bifasciatum*. All of these species showed higher frequencies than expected of being chased by damselfish in the peripheral regions of their home ranges; thus suggesting their core use areas may

provide refuge from damselfish encounters.

High degrees of ontogenetic and heterospecific overlap in microhabitat use and behaviour

Extensive ontogenetic and heterospecific overlap was found among these labrids (Chapter III and V). In some cases, conspecifics of different life stages were less similar than heterospecifics of the same life stage. In other words, heterospecific terminal phase individuals are much more similar in behaviour and microhabitat use than TP individuals are to conspecific juveniles. The most consistent observation (through multiple methods of behavioural observations) was that as labrids grow, they spend more time swimming alone, and less time hovering with their tails curled and touching their noses to the substrate (Chapter III). Social interactions are notably important for these labrids. Even to first-time visitors to a coral reef environment, the extremely social behaviour of these fishes is readily apparent. Aggregative behaviour by animals can increase feeding opportunities for the attendants (Diamant and Shpigel 1985, Aronson and Sanderson 1987, Sikkel and Hardison 1992, Baird 1993, Matsumoto et al. 1999). Schooling behaviour is also recognized as an anti-predator mechanism (Ehrlich and Ehrlich 1973, Magurran and Seghers 1990, Coulson 1999). Furthermore, mixed-species' schooling in herbivorous coral reef fishes has been related to avoidance of attacks from territorial damselfish that defend an algal mat (Barlow 1974, Robertson et al. 1976, Foster 1985). Labrids are often found in mixed-species' foraging groups with parrotfish (Scaridae), surgeonfish (Acanthuridae), and butterflyfish (Chaetodontidae). This behaviour may allow labrids to gain access to damselfish eggs.

With respect to microhabitat use, the most consistent finding was the ontogenetic increase in the use of topographically simple microhabitats (Chapter V). Terminal phase adults of the labrids in this study showed higher use of sand microhabitats than conspecific juveniles and IP adults. There were some differences among the species with respect to microhabitat use; however, there was a high degree of variability among individuals within a species, and differences in

microhabitat use were not substantial enough to strongly predict group membership through discriminant function analysis.

Overall, there were very high degrees of similarity among these labrid species and their life stages with respect to behaviour and microhabitat use. How, then, can such ecologically similar fishes coexist? Several factors that may operate independently or concurrently in this system may enable coexistence of these sympatric labrids.

Factors that potentially promote coexistence

The coexistence of ecologically similar, closely-related fishes on coral reefs has been explained by four major groups of hypotheses: 1) niche diversification, 2) the competitive lottery hypothesis, 3) recruitment limitation, and 4) predation or disturbance limitation (reviewed by Ebeling and Hixon 1991). In a study similar to the present study, Overholtzer and Motta (1999) found no evidence of resource partitioning in terms of food or space in three juvenile parrotfish species (Scaridae). They concluded that their observations did not support conventional models of niche diversification through past or present interspecific competition. They suggested that alternatively, 1) resources may not be limited for these parrotfish juveniles, or 2) these fishes are competing and a non-equilibrium mechanism such as limitation by recruitment, abiotic disturbance, or predation allows them to coexist. Because niche diversification does not appear to be a primary explanation of coexistence for the labrids in this study, the alternatives suggested by Overholtzer and Motta (1999) may be applicable; however, there may be other factors operating. Outside of coral reef literature, there have been several other perspectives regarding factors that promote coexistence, for example, centrifugal habitat organization (Rosenzweig and Abramsky 1986, Chesson and Rosenzweig 1991).

Centrifugal habitat organization (Rosenzweig and Abramsky 1986) occurs because it is not uncommon in nature for some habitats to be favored over other habitats by all species (Chesson

and Rosenzweig 1991). Centrifugal habitat organization simply refers to the flexible use of marginal habitat by the coexisting species, which does not result in strict segregation of species. Coral reef environments are extremely heterogeneous at multiple spatial scales. Labrids show high variability and flexibility in microhabitat use (Chapter V), therefore centrifugal habitat organization may be occurring.

The effect of territorial pomacentrids on labrids

It was observed in Chapter III and Chapter VI that territorial pomacentrids affect the spatial arrangements, behaviours, and social interactions of labrids. Interference competition between labrids and pomacentrids has negative implications for labrid time budgets of behavior (Chapter VI). Community surveys revealed very high population densities of pomacentrids (Chapter VII), and uni-specific colonies of pomacentrids were observed in St. Croix, similar to those described by Itzkowitz (1977b). How, then, can labrids also be so abundant in these locations? High densities of pomacentrids may actually alleviate interspecific competition exerted on labrids by pomacentrids, as intraspecific aggregation in patchy environments can promote coexistence (Atkinson and Shorrocks 1984, Ives and May 1985, Ives 1988, Inouye 1999). According to Inouye (1999), if a superior competitor (i.e., pomacentrids) is aggregated so that some patches harbour many individuals while others harbour few, then an inferior competitor (i.e., labrids) using the same set of patches may persist indefinitely. As aggregation of the superior competitor increases, the superior competitor suffers more from intraspecific competition, and a higher proportion of patches are left empty for inferior competitors to exploit.

Local mechanisms that generate patterns in labrid assemblage structure at larger scales

Although agonistic interactions between territorial pomacentrids and labrids appears to be a main factor affecting the spatial arrangement of labrid home ranges (Chapter III, and VI), it is not a primary factor affecting patterns of labrid distribution on a scale larger than that of the

individual home range (Chapter VII). The environmental factor that exhibited the largest effect on labrid assemblage structure was zonation. Within a reef, some labrid species and their life stages demonstrated strong negative or positive associations with environmental features. These microhabitat associations on a larger spatial scale sometimes agreed with microhabitat associations found on more localized spatial scales (i.e., that of the individual home range). The only strong relationship between pomacentrids and labrids was a strong negative association in the back reef data set between several *Halichoeres* species and the beaugregory damselfish. Many interactions or processes that in theory could influence population dynamics in practice fail to produce measurable effects upon population dynamics (Adler and Morris 1994).

Significance of the dissertation

All of the studies described in this dissertation were natural observations conducted *in situ* on continuous coral reefs instead of patch reefs around St. Croix, U.S.V.I. Two benefits of these methods are: 1) there are many differences between observations made on captive individuals and those left in their natural environment (Ehrlich 1975, Goldman and Talbot 1976, Sale 1980), and 2) there is an increasing awareness that findings from studies conducted on patch reefs often do not scale up to explain the dynamics on continuous reefs (e.g. Zeller 1997, Syms 1998).

Another feature of this dissertation is that it combined “mechanistic” explanations with “correlative” explanations. Mechanistic explanations are explanations for which an actual mechanism has been tested and confirmed as likely (Chapter VI). Correlative explanations reveal patterns or relationships, such as relationships between environmental variables and labrid variables (Chapter VII).

Additionally, this dissertation involves several levels of complexity, from simple observations of single individuals, to ontogenetic comparisons within a single species, to comparisons across six species, to larger community-level investigations. Ontogenetically, at each

size, a fish is likely to have a different set of competitors and predators, different behaviours (Chapter II) and microhabitat requirements (Chapter V). These differences can produce an incredibly complex set of interactions and behavioural dynamics within a community containing even a small number of species (Helfman et al. 1997). Furthermore, the dynamics of communities are potentially exceedingly complicated (Godfray and Blythe 1990). Despite the complexities, several conclusions were drawn from each level.

Although the labrids involved in these studies are not commercially important, there are many other labrid species around the world that are (e.g. *Labrus merula* on the Adriatic coast (Dulcic et al. 1999), and *Coris julis* in the Mediterranean (Lejeune 1987)). The approaches used to address questions of spatial arrangements in this thesis could be applied to commercially important species or endangered species.

Future research directions

There are many tangential studies in this dissertation that will be developed in the future. For example, the effect of microhabitat configuration on the shape of home range boundaries has not been fully investigated. Gerking (1994) suggests that all fish home ranges are irregular in shape, and these irregularities can often be explained by irregularities in microhabitat, such as contours of rocks or corals. The effect of microhabitat on the position of activity centers within home ranges could also be considered. Labrids show such high degrees of variability in microhabitat use within a species (Chapter V), that it is doubtful if such subtleties as microhabitat contours would explain the differences in home range shape or position of activity centers within home ranges. But this remains to be investigated.

A second tangential study leading from this dissertation is to use the empirical data to support or modify theoretical models. There are several applicable models to this system. One possibility is to model the effects of competition on natal dispersal distance (McCarthy (1999)

(where competitors would be territorial pomacentrids, natal sites would be the initial settlement sites of labrids, and natal dispersal would be home range relocation). Another factor in home range dynamics that has yet to be investigated and is critical to spatial modelling is how often individuals relocate (except see Frederick 1997). Is there preemptive site occupancy with the tendency for individuals to move to sites of higher quality as they become available (Rodenhouse et al. 1997)?

Another possibility is to model the spatial dynamics of labrids and how they are affected by the composition of their neighbours by modifying a habitat model from Stamps et al. (1987) who looked at “hard-edge” boundaries (unfavorable microhabitats) versus “soft-edge” boundaries (favourable microhabitats). This could also be employed as a social interaction model. Hard-edge boundaries would be exemplified by a boundary between a pomacentrid and a labrid, and a soft-edge boundary would be exemplified by a boundary between two labrids. Stamps et al. (1987) used a computer simulation that looked at the effect of habitat geometry on intruder pressure for territories. They then modeled the shifts in territory size and characteristics. In their model, habitat heterogeneity provided “sinks” which caused shifts in home ranges. Habitat heterogeneity parallels the heterogeneous configurations of neighbours on coral reefs. “Sinks” would occur when a neighbouring fish emigrates or dies, and “reserves” would be similar to the arrival of a new settlers to reef habitats. This dissertation opens many doors to future investigations of labrid species.

LITERATURE CITED

- Abrams, P. 1983. The theory of limiting similarity. *Ann. Rev. Ecol. Syst.* 14:359-376.
- Adjeroud, M., Y. Letourneur, M. Porcher, and B. Salvat. 1998. Factors influencing spatial distribution of fish communities on a fringing reef at Mauritius, S.W. Indian Ocean. *Env. Biol. Fish.* 53: 169-182.
- Adler, F.R., and W.F. Morris. 1994. A general test for interaction modification. *Ecology*. 75(6): 1552-1559.
- Alberts, A.C. 1993. Relationship of space use to population density in an herbivorous lizard. *Herpetologica*. 49: 469-479.
- Alevizon, W.S., R. Richardson, P. Pitts, and G. Serviss. 1985. Coral zonation and patterns of community structure in Bahamian reef fishes. *Bull. Mar. Sci.* 36(2): 304-318.
- Allen, G.R. 1991. Damselfishes of the world. Mergus Publishers, Hong Kong. 271pp.
- Allen, R.L., and D.M. Baltz. 1997. Distribution and microhabitat use by flatfishes in a Louisiana estuary. *Env. Biol. Fish.* 50(1): 85-103.
- Anderson, D.J. 1982. The home range: a new nonparametric estimation technique. *Ecology*. 63(1): 103-112.
- Anderson, T.W. 1994. Role of macroalgal structure in the distribution and abundance of a temperate reef fish. *Mar. Ecol. Prog. Ser.* 3:279-296.
- Anderson, T.W., E.E. DeMartini, and D.A. Roberts. 1989. The relationship between habitat structure, body size and distribution of fishes at a temperate artificial reef. *Bull. Mar. Sci.* 44:681-697.
- Anonymous. 1969. Virgin Islands Ecological Research Station. Special Report: Study of the Fisheries Potential of the Virgin Islands. Contribution #1. Caribbean Research Center.
- Aparicio, E., and A. de Sostoa. 1999. Pattern of movements of adult *Barbus haasi* in a small Mediterranean stream. *J. of Fish Biol.* 55: 1086-1095.
- Aronson, R.B., and S.L. Sanderson. 1987. Benefits of heterospecific foraging by the Caribbean wrasse, *Halichoeres garnoti* (Pisces: Labridae). *Env. Biol. Fish.* 18: 303-308.
- Atkinson, W.D., and B. Shorrocks. 1984. Aggregation of larval Diptera of discrete and

- ephemeral breeding sites: the implications for coexistence. *Am. Nat.* 124(3): 336-351.
- Ault, T.R. and C.R. Johnson. 1998. Spatially and temporally predictable fish communities on coral reefs. *Ecol. Monogr.* 68: 25-50.
- Auster, P.J., R.J. Malatesta, and C.L.S. Donaldson. 1997. Distributional responses to small-scale habitat variability by early juvenile silver hake, *Merluccius bilinearis*. *Env. Biol. Fish.* 50: 195-200.
- Balon, E.K. 1975. Reproductive guilds of fishes: a proposal and definition. *J. Fish. Res. Board. Can.* 32: 821-864.
- Baltz, D.M., P.B. Moyle, and N.J. Knight. 1982. Competitive interactions between benthic stream fishes, riffle sculpin, *Cottus gulosus*, and speckled dace, *Rhinichthys osculus*. *Can. J. Fish. Aquat. Sci.* 39: 1502-1511.
- Baird, T.A. 1993. A new heterospecific foraging association between the puddingwife wrasse, *Halichoeres radiatus*, and the bar jack, *Caranx ruber*: evaluation of the foraging consequences. *Env. Biol. Fish.* 38: 393-397.
- Baras, W. 1997. Environmental determinants of residence areas selection by *Barbus barbus* in the River Ourthe. *Aquat. Living. Resour.* 10: 195-206.
- Bardach, J.E. 1958. On the movements of certain Bermuda reef fishes. *Ecology.* 29(1): 139-146.
- Barlow, G.W. 1974a. Contrasts in social behavior between Central American cichlid fishes and coral reef surgeon fishes. *Amer. Zool.* 14:9-34.
- Barlow, G.W. 1974b. Extraspecific imposition of social grouping among surgeonfishes (Pisces: Acanthuridae). *J. Zool. Lond.* 174: 333-340.
- Barlow, G.W. 1975. On the sociobiology of some hermaphroditic serranid fishes, the hamlets, in Puerto Rico. *Mar. Biol.* 33: 295-300.
- Barrett, N.S. 1995. Short- and long-term movement patterns of six temperate reef fishes (Families Labridae and Monacanthidae). *Mar. Freshwater Res.* 46: 853-860.
- Barrett, N.S. 1999. Food availability is not a limiting factor in the growth of three Australian temperate reef fishes. *Env. Biol. Fish.* 56: 419-428.
- Barrows, E.M. 1996. Animal behaviour desk reference, second printing. C.R.C. Press. Boca Raton. 672pp.
- Behrents, K.C. 1987. The influence of shelter availability on recruitment and early juvenile survivorship of *Lythrypnus dalli* Gilbert (Pisces: Gobiidae). *J. Exp. Mar. Biol. Ecol.* 107:45-59.

- Bell, J.D., G.J.D. Craik, D.A. Pollard, and B.C. Russell. 1985. Estimating length frequency distributions of large reef fish underwater. *Coral Reefs*. 4: 41-44.
- Bell, J.D., and R. Galzin. 1984. Influence of live coral cover on coral reef fish communities. *Mar. Ecol. Prog. Ser.* 15: 265-274.
- Bell, J., M. Harmelin-Vivien, and R. Galzin. 1985. Large-scale spatial variation in abundance of butterflyfishes (Chaetodontidae) on Polynesian reefs. *Proc. 5th Int. Coral Reef Congr., Tahiti*. 5: 421-426.
- Bellwood, D.R. 1988. Ontogenetic changes in the diet of early post-settlement *Scarus* species (Pisces: Scaridae). *J. Fish. Biol.* 33: 213-219.
- Bertram, B.C.R. 1978. Living in groups: predators and prey. Pp. 64-96, in: *Behavioural Ecology: an evolutionary approach*. (J.R. Krebs and N.B. Davies, eds.). Blackwell, Oxford, UK.
- Bohlke, J.E. and Chaplin, C.C.G. 1968. *Fishes of the Bahamas and adjacent tropical waters*. Wynnewood, Pa. 771pp. 2nd Edition (1993)
- Bohnsack, J.A. 1982. Effects of piscivorous predator removal on coral reef fish community structure. *Fish Food Habit Studies*. *Proc. Third. Workshop*. C.A. Simenstad, eds. Washington Sea Grant Publication. U. of Washington, Seattle.
- Booth, D.J., and G.A. Beretta. 1994. Seasonal recruitment, habitat associations, and survival of pomacentrid reef fish in the US Virgin Islands. *Coral Reefs*. 13: 81-89.
- Bouchon-Navaro, Y., and C. Bouchon. 1989. Correlations between chaetodontid fishes and coral communities of the Gulf of Aqaba (Red Sea). *Env. Biol. Fish.* 25: 47-60.
- Bouchon-Navaro, Y. and M.L. Harmelin-Vivien. 1981. Quantitative distribution of herbivorous reef fishes in the Gulf of Aqaba (Red Sea). *Mar. Biol.* 63: 79-86.
- Boulding, E.G. and K.L. VanAlstyne. 1993. Mechanisms of differential survival and growth of two species of *Littorina* on wave exposed and on protected shores. *J. Exp. Mar. Biol. Ecol.* 169:139-188.
- Boutin, J.L., and G.H. Orians. 1970. Spacing patterns in mobile animals. *Ann. Rev. Ecol. Syst.* 1: 239-262.
- Brandt, C.A., J.K. Parrish, and C.N. Hodges. 1995. Predictive approaches to habitat quantification: Dark-rumped petrels on Haleakala, Maui. *Auk*. 112(3):571-579.
- Bradbury, C., J.M. Green, and M. Bruce-Lockhart. 1995. Home ranges of female cunner, *Tautoglabrus adspersus* (Labridae), as determined by ultrasonic telemetry. *Can. J. Zool.* 73: 1268-1279.
- Braithwaite, V.A. 1998. Spatial memory, landmark use and orientation in fish. Ch. 5. *In: Spatial*

- Representation in Animals. Ed. S. Healy. Oxford University Press, New York, U.S.A.
- Bray, R.N., A.C. Miller, and G.G. Geesey. 1981. The fish connection: a trophic link between planktonic and rocky reef communities? *Science*. 214 (Oct. 9): 204-205.
- Breder C.M. 1959. Studies on social groupings in fish. *Bull. Am. Mus. Nat. Hist.* 117: 399-481.
- Brothers, E.B., and W.N. McFarland. 1981. Correlations between otolith microstructure, growth, and life history transitions in newly recruited French grunts (*Haemulon flavolineatum* (Desmarest), Haemulidae). *Rapports Proces- Verbaux Reunions conseil International l'Exploration Mer.* 178:369-374.
- Brown, J.L. 1969. Territorial behavior and population regulation in birds. *Wilson Bull.* 81: 533-537.
- Brown, J.H. 1971. Mechanisms of competitive exclusion between two species of chipmunks. *Ecology*. 52(2): 305-311.
- Buchheim, J.R., and M.A. Hixon. 1992. Competition for shelter holes in the coral reef fish *Acanthemblemaria spinosa* Metzelaar. *J. Exp. Mar. Bio. Ecol.* 164:45-54.
- Budaev, S.V. 1997. Alternative styles in the European wrasse, *Symphodus ocellatus*: boldness-related schooling tendency. *Env. Biol. Fishes.* 49: 71-78.
- Burt, W.H. 1943. Territoriality and home range concepts as applied to mammals. *J. Mammal.* 24: 346-352.
- Caley, J.M. 1995. Community dynamics of tropical reef fish: local patterns between latitudes. *Mar. Ecol. Prog. Ser.* 129: 7-18.
- Caley, M.J., and J. St. John. 1996. Refuge availability structures assemblages of coral reef fishes. *J. Anim. Ecol.* 65: 414-428.
- Cantrell, R.S., and C. Cosner. 1999. Diffusion models for population dynamics incorporating individual behaviour at boundaries: applications to refuge design. *Theor. Pop. Biol.* 55: 189-207.
- Carpenter, K.E., R.I. Mical, V.D. Albaladejo, and V.T. Corpuz. 1981. The influence of substrate structure on the local abundance and diversity of Philippine reef fishes. *Proc. Fourth Int. Coral Reef Symp., Manila.* 2: 497-502.
- Carr, M.H. 1989. Effects of macroalgal assemblages on the recruitment of temperate zone reef fishes. *J. Exp. Mar. Biol. Ecol.* 126:59-76.
- Carr, M.H., and M.A. Hixon 1995. Predation effects on early post-settlement survivorship of coral-reef fishes. *Mar. Ecol. Prog. Ser.* 124: 31-42.

- Caselle, J.E., and R.R. Warner. 1996. Variability in recruitment of coral reef fishes: the importance of habitat at two spatial scales. *Ecology*. 77(8): 2488-2504.
- Chesson, P., and M. Rosenzweig. 1991. Behavior, heterogeneity, and the dynamics of interacting species. *Ecology*. 72(4): 1187-1195.
- Chilton, E.W., and S.M. Poarch. 1997. Distribution and movement behavior of radiotagged grass carp in two Texas reservoirs. *Trans. Am. Fish. Soc.* 126: 467-476.
- Chittaro, P.M. 2000. The effects of spatial scale on the structure on coral reef fish populations and assemblages. M.Sc. Thesis. University of Windsor.
- Choat, J.H., A.M. Ayling, and D.R. Schiel. 1988. Temporal and spatial variation in an island fish fauna. *J. Exp. Mar. Biol. Ecol.* 121: 91-111.
- Christian, K.A. and S. Waldschmidt. 1984. The relationship between lizard home range and body size: A reanalysis of the data. *Herpetologica*. 40: 68-75.
- Clark, W.C., and M. Mangel. 1986. The evolutionary advantages of group foraging. *Theor. Pop. Biol.* 30: 45-75.
- Clarke, R.D. 1977. Habitat distribution and species diversity of Chaetodontid and Pomacentrid fishes near Bimini, Bahamas. *Mar. Biol.* 40:277-289.
- Clarke, M.F., K., Burke da Silva, H. Lair, R. Pocklington, D.L. Kramer, and R.L. McLaughlin. 1993. Site familiarity affects escape behavior of the eastern chipmunk, *Tamias striatus*. *Oikos*. 66: 533-537.
- Cohen, M.A., W.R.C. Beaumont, and N.C. Thorp. 1999. Movement and activity patterns of the black piranha. *Env. Biol. Fish.* 54: 45-52.
- Cole, K.S. 1984. Social spacing in the temperate marine goby *Coryphopterus nicholsi*. *Mar. Biol.* 80: 307-314.
- Coleman, K., and D.S. Wilson. 1996. Behavioral and ecological determinants of home range size in juvenile pumpkinseed sunfish (*Lepomis gibbosus*). *Ethology*. 102: 900-914.
- Connell, J.H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Am. Nat.* 111: 1119-1144.
- Connell, S.D. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos*, 35: 131-138.
- Connell, S.D., and G.P. Jones. 1991. The influence of habitat complexity on postrecruitment processes in a temperate reef fish population. *J. Exp. Mar. Biol. Ecol.* 151: 271-294.
- Connor, E.F., and D. Simberloff. 1979. The assembly of species communities: chance or

- competition? *Ecology*. 60(6): 1132-1140.
- Coulson, G. 1999. Monospecific and heterospecific grouping and feeding behavior in grey kangaroos and red-necked wallabies. *J. Mammology*. 80(1): 270-282.
- Cowie, R.H. 1985. Microhabitat choice and high temperature tolerance in the land snail *Theba pisana* (Mollusca: Gastropoda). *J. Zool. London (A.)* 207:201-211
- Cowlshaw, G. 1999. Ecological and social determinants of spacing behaviour in desert baboon groups. *Behav. Ecol. Sociobiol.* 45: 67-77.
- Cox, E.F. 1994. Resource use by corallivorous butterflyfishes (family Chaetodontidae) in Hawaii. *Bull. Mar. Sci.* 54: 535-545.
- Crowe, T. 1996. Different effects of microhabitat fragmentation on patterns of dispersal of an intertidal gastropod in two habitats. *J. Exp. Mar. Biol. Ecol.* 206:83-107.
- Damuth, J. 1981. Home range, home range overlap, and species energy use among herbivorous mammals. *Biol. J. Linn. Soc.* 15: 185-193.
- Danilowicz, B.S. 1995. Spatial patterns of spawning in the coral reef damselfish *Dascyllus albisella*. *Mar. Biol.* 122:145-155.
- Davies, N.B., and A.I. Houston. 1984. Territory economics. In *Behavioural Ecology. An Evolutionary Approach*. 148-169. Krebs, J.R., and Davies, N.B. (Eds.). Oxford: Blackwell Scientific Publications.
- deBoer, B.A. 1978. Factors influencing the distribution of the damselfish *Chromis cyanea* (Poey), Pomacentridae, on a reef at Curacao, Netherlands Antilles. *Bull. Mar. Sci.* 28: 550-565.
- deJong, G. 1979. The influence of the distribution of juveniles over patches of food on the dynamics of a populations. *Netherlands J. Zool.* 29(1): 33-51.
- de Martini, E.E. 1998. How might recruitment research on coral reef fishes help manage tropical reef fishes? *Aust. J. of Ecol.* 23: 305-310.
- de Martini, E.E., D.A. Roberts. 1990. Effects of giant kelp (*Macrocystis*) on the density and abundance of fishes in a cobble-bottom kelp forest. *Bull. Mar. Sci.* 46:287-300.
- Deslippe, R.J., and R.T. M'Closkey. 1991. An experimental test of mate defense in an iguanid lizard (*Sceloporus graciosus*). *Ecology*. 72: 1218-1224.
- de Solla, S.R., R. Bonduriansky, and R.J. Brooks. 1999. Eliminating autocorrelation reduces biological relevance of home range estimates. *J. Anim. Ecol.* 68: 221-234.
- deVries, D.R., R.A. Stein, J.G. Miner, and G.G. Mittelbach. 1991. Stocking threadfin shad: consequences for young-of-year fishes. *Trans. Am. Fish. Soc.* 120: 368-381.

- Diamant, A., and M. Shpigel. 1985. Interspecific feeding association of groupers (Teleostei: Serranidae) with octopuses and moray eels in the Gulf of Eilat (Aqaba). *Env. Biol. Fish.* 13: 153-159.
- Dill, L.M., R.C. Ydenberg, and A.H.G. Fraser. 1981. Food abundance and territory size in juvenile coho salmon (*Oncorhynchus kisutch*). *Can. J. Zool.* 59: 1801-1809.
- Doherty, P.J. 1983. Tropical territorial damselfishes: is density limited by aggression or recruitment? *Ecology*. 64: 176-190.
- Doherty, P.J. 1987. The replenishment of populations of coral reef fishes, recruitment surveys, and the problems of variability manifest on multiple scales. *Bull. Mar. Sci.* 41: 411-422.
- Doherty, P.J. 1991. Spatial and temporal patterns in recruitment. In: Sale, P.F. (ed.) *The ecology of fishes on coral reefs*. Academic Press, San Diego. 261-293.
- Doherty, P.J., and T. Fowler. 1994. An empirical test of recruitment limitation in a coral reef fish. *Science*. 263: 935-939.
- Doherty, P.J., and P.F. Sale. 1985. Predation on juvenile coral reef fishes: an exclusion experiment. *Coral Reefs*. 4: 225-234.
- Doherty, P.J., and D.McB. Williams. 1988. The replenishment of coral reef fish populations. *Oceanogr. Mar. Biol. Annu. Rev.* 26: 487-551.
- Dulcic, J., V. Kozul, M. Kraljevic, B. Skaramuca, B. Glamuzina, and P. Re. 1999. Embryonic and larval development of the brown wrasse *Labrus merula* (Pisces: Labridae). *J. Mar. Biol. Ass. U.K.* 79: 327-332.
- Eason, P.K., and J.A. Stamps. 1992. The effect of visibility on territory size and shape. *Behav. Ecol.* 3: 166-172.
- Ebeling, A.W., M.A. Hixon. 1991. Tropical and temperate reef fishes: a comparison of community structures. In: Sale, P.F. (Ed.) *The ecology of fishes on coral reefs*. Academic Press, San Diego, C.A. 509-563.
- Ebersole, J.P. 1977. The adaptive significance of interspecific territoriality in the reef fish *Eupomacentrus leucostictus*. *Ecology*. 58:914-920.
- Ebersole, J.P. 1980. Food density and territory size: alternative model and a test on the reef fish *Eupomacentrus leucostictus*. *Am. Nat.* 115: 492-509.
- Ebersole, J. P. 1985. Niche separation of two damselfish species by aggression and differential microhabitat utilization. *Ecology* 66(1): 14-20.
- Eckert, G.J. 1987. Estimates of adult and juvenile mortality for labrid fishes at One Tree Reef, Great Barrier Reef. *Mar. Biol.* 95: 167-171.

- Eggleston, D.B. 1995. Recruitment in Nassau grouper, *Epinephelus striatus*: post-settlement abundance, microhabitat features and ontogenetic habitat shifts. *Mar. Ecol. Prog. Ser.* 124:9-22.
- Ehrlich, P.R., and A.H. Ehrlich. 1973. Coevolution: heterotypic schooling in Caribbean reef fishes. *Am. Nat.* 107: 157-160.
- Ehrlich, P.R. 1975. The population ecology of coral reef fishes. *Ann. Rev. Ecol. Syst.* 6:211-247.
- Eifler, D.A. 1996. Experimental manipulation of spacing patterns in the widely foraging lizard *Cnemidophorus uniparens*. *Herpetologica*. 52(4): 477-486.
- Evans, E.W. 1991. Intra versus interspecific interactions of ladybeetles (Coleoptera: Coccinellidae) attacking aphids. *Oecologia*. 87: 401-408.
- Fedderm, H.A. 1965. The spawning, growth, and general behavior of the bluehead wrasse, *Thalassoma bifasciatum* (Pisces: Labridae). *Bull. Mar. Sci.* 15: 896-941.
- Feinsinger, P., E.E. Spears, and R.W. Poole. 1981. A simple measure of niche breadth. *Ecology*. 62(1): 27-32.
- Ferreira, C.E.L., J.E.A. Goncalves, R. Continho, and A.C. Peter. 1998. Herbivory by the dusky damselfish *Stegastes fuscus* (Cuvier, 1830) in a tropical rocky shore: effects on the benthic community. *J. Exp. Mar. Biol. Ecol.* 229: 241-264.
- Findley, J.S., and M.T. Findley. 1985. A search for pattern in butterflyfish communities. *Am. Nat.* 126: 800-816.
- Fishelson, L. 1977. Sociobiology of feeding behavior of coral reef fish among the coral reef of gulf Eilat (= gulf Aqaba), Red Sea. *Israel J. Zool.* 26: 114-134.
- Fishelson, L., D. Popper and A. Avidor. 1974. Biosociology and ecology of pomacentrid fishes around the Sinai Peninsula. *J. Fish Biol.* 6:119-133.
- Fitch, W.T.S., and D.Y. Shapiro. 1990. Spatial dispersion and nonmigratory spawning in the bluehead wrasse (*Thalassoma bifasciatum*). *Ethology*. 85: 199-211.
- Forrester, G. E. 1990 Factors influencing the juvenile demography of a coral reef fish. *Ecology* 71(5): 1666-1681.
- Forrester, G.E. 1995. Strong density-dependent survival and recruitment regulate the abundance of a coral reef fish. *Oecologia*. 103: 275-282.
- Foster, S.A. 1985. Group foraging by a coral reef fish: a mechanism for gaining access to defended resources. *Anim. Behav.* 33: 782-792.

- Fowler, A.J. 1990. Spatial and temporal patterns of distribution and abundance of chaetodontid fishes at One Tree Reef, southern GBR. *Mar. Ecol. Prog. Ser.* 64: 39-53.
- Frederick, J.L. 1997. Post-settlement movement of coral reef fishes and bias in survival estimates. *Mar. Ecol. Prog. Ser.* 150: 65-74.
- Freeman, S., and W. Alevizon. 1983. Aspects of territorial behavior and habitat distribution of the fairy basslet *Gramma loreto*. *Copeia*. 1983(3): 829-832.
- French, B.W. 1999. Temporal and spatial distribution of ground beetle (Coleoptera: Carabidae) assemblages in grasslands and adjacent wheat fields. *Pedobiologia*. 43: 73-84.
- Fretwell, S.D., and H.L. Lucas. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta. Biotheor.* 19:16-35.
- Fricke, H.W. 1975. Evolution of social systems through site attachment in fish. *Z. Tierpsychol.* 39:206-210.
- Froese, R., and D. Pauly. Editors. 1999. FishBase 99. World Wide Web electronic publication. www.fishbase.org. 25 May 2000.
- Funk, J.L. 1955. Movement of stream fishes in Missouri. *Trans. Am. Fish. Soc.* 85: 39-57.
- Fryxell, J.M., and P. Lundberg. 1998. Individual behavior and community dynamics. Chapman and Hall. New York, New York. U.S.A. 197pp.
- Gallerani Lawson, E.J. and A.R. Rodgers. 1997. Differences in home-range size computed in commonly used software programs. *Wildlife Soc. Bull.* 25(3): 721-729.
- Garcia Berthou, E. 1999a. Food of introduced mosquitofish: Ontogenetic diet shift and prey selection. *J. Fish Biol.* 55(1): 135-147.
- Garcia Berthou, E. 1999b. Spatial heterogeneity in roach (*Rutilus rutilus*) diet among contrasting basins within a lake. *Archiv. fuer Hydrobiologie*. 146(2): 239-256.
- Garvey, J.E., and R.A. Stein. 1998. Competition between larval fishes in reservoirs: the role of relative timing of appearance. *Trans. Am. Fish. Soc.* 127: 1021-1039.
- Gerking, S.D. 1994. Feeding Territory. Ch. 10 In: *Feeding Ecology of Fish*. Academic Press. California, U.S.A. pp. 223-241.
- Gerking, S.D. 1994. *Feeding Ecology of Fish*. Academic Press. California, U.S.A.
- Gladfelter, W.B., and E.H. Gladfelter 1978. Fish community structure as a function of habitat structure on West Indian patch Reefs. *Rev. Biol. Trop.* 26:65-84.
- Gladfelter, W.B., J.C. Ogden, and E.H. Gladfelter. 1980. Similarity and diversity among coral

- reef fish communities: a comparison between tropical western Atlantic (Virgin Islands) and tropical central Pacific (Marshall Islands) patch reefs. *Ecology*. 61: 1156-1168.
- Godfray, H.C.J. and S.P. Blythe. 1990. Complex dynamics in multispecies communities. *Phil. Trans. R. Soc. Lond. B*. 330:221-233.
- Goforth, R.R., and J.W. Foltz. 1998. Movements of the yellowfin shiner, *Notropis lutipinnis*. *Ecol. Freshwater Fish*. 7: 49-55.
- Goldman, B., and F.H. Talbot. 1976. Aspects of the ecology of coral reef fishes. Pp. 125-154 In: O.A. Jones and R. Endean (eds.) *Biology and Geology of Coral Reefs*. Vol. 3. Academic Press, New York.
- Gomelyuk, V.E. and Leunov. 1999. Changes in age-specific behaviour and spatial structure of masked greenling, *Hexagrammus octogrammus* (Hexagrammidae). *Env. Biol. Fish*. 54: 313-323.
- Gomez, E.D., W.Y. Licuanan, and V.V. Hiloma. 1988. Reef fish benthos correlations in the northwestern Philippines. *Proc. 6th Int. Coral Reef Symp.* 3: 245-249.
- Gordon, D.M. 1997. The population consequences of territorial behavior. *TREE*. 12(2): 63-66.
- Green, A.L. 1992. Damselfish territories: the focal sites for studies of the early life history of labroid fishes. *Proc. 7th Int. Coral Reef Symp.* 1: 601-605.
- Green, A.L. 1996. Spatial, temporal and ontogenetic patterns of habitat use by coral reef fishes (family Labridae). *Mar. Ecol. Prog. Ser.* 133 (1-3): 1-11.
- Gregory, R.S., and J.T. Anderson. 1997. Substrate selection and use of protective cover by juvenile Atlantic cod, *Gadhus morhua* in inshore waters of Newfoundland. *Mar. Ecol. Prog. Ser.* 146: 9-20.
- Grigg, R.W. 1994. Effects of sewage discharge, fishing pressure and habitat complexity on coral ecosystems and reef fishes in Hawaii. *Mar. Ecol. Prog. Ser.* 103: 25-34.
- Gross, M.R., and A. MacMillan. 1981. Predation and the evolution of colonial nesting in bluegill sunfish (*Lepomis macrochirus*). *Behav. Ecol. Sociobiol.* 8: 163-174.
- Grossman, G.D. 1982. Community and patterns of resource partitioning. *Proc. 3rd. Pacific Workshop*. Washington Sea Grant Publication.
- Gutierrez, L. 1996. Coexistence of coral reef fishes: the role of recruitment and post-recruitment processes. PhD Thesis, University of Houston.
- Hairston, N.G., F.E. Smith, and L.B. Slobodkin. 1960. Community structure, population control and competition. *Am. Nat.* 44: 421-425.

- Hall, D.J. and E.E. Werner. 1977. Seasonal distribution of fishes in the littoral zone of a Michigan lake. *Trans. Amer. Fish. Soc.* 106:545-555.
- Harmelin-Vivien, M.L. 1989. Implications of feeding specialization on the recruitment processes and community structure of butterflyfishes. *Env. Bio. Fish.* 25: 101-110.
- Hart, A.M., D.W. Klumpp, and G.R. Russ. 1996. Response of herbivorous fishes to crown-of-thorns *Acanthaster planci* outbreaks. II. Density and biomass of selected species of herbivorous fish and fish-habitat correlations. *Mar. Ecol. Prog. Ser.* 132: 21-30.
- Helfman, G.S., and E.T. Schultz. 1984. Social transmission of behavioural information in a coral reef fish. *Anim. Behav.* 32: 379-384.
- Helfman, G.S. 1994. Adaptive variability and mode choice in foraging fishes, in *Theory and Application in Fish Feeding Ecology*, (eds. D.J. Stouder, K.L. Fresh, and T.J. Feller). U. of South Carolina Press. Pp 3-17.
- Helfman, G.S., B.B. Collette, and D.E. Facey. 1997. *The Diversity of Fishes*. Blackwell Scientific. Mass., U.S.A.
- Hews, D.L. 1993. Food resources affect female distribution and male mating opportunities in the iguanian lizard *Uta palmeri*. *Anim. Behav.* 46: 279-291.
- Hixon, M. A. 1991. Predation as a process structuring coral reef fish communities. Ch. 17 In: P.F. Sale (ed.) *The Ecology of Fishes on Coral Reefs*. Academic Press, Inc.
- Hixon, M.A., and J.P. Beets. 1993. Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecol. Monogr.* 63: 77-101.
- Hixon, M.A., and B.A. Menge. 1991. Species diversity: prey refuges modify the interactive effects of predation and competition. *Theor. Pop. Biol.* 39: 178-200.
- Hoffman, S.G. 1983. Sex-related foraging behaviour in sequentially hermaphroditic hogfishes. *Ecology.* 64: 798-808.
- Hoines, A.S. and O.A. Bergstad. 1999. Resource sharing among cod, haddock, saithe and pollack on a herring spawning ground. *J. Fish. Biol.* 55 (6): 1233-1257.
- Holbrook, S.J., M.H. Carr, R.J. Schmitt, and J.A. Coyer. 1990. Effect of giant kelp on local abundance of reef fishes: the importance of ontogenetic resource requirements. *Bull. Mar. Sci.* 47(1): 103-114.
- Holbrook, S.J., M.J. Kingsford, R.J. Scmitt, and J.S. Stephens. 1994. Spatial and temporal patterns in assemblages of temperate reef fish. *Amer. Zool.* 34: 463-475.
- Holland, K.N., J.D. Peterson, C.G. Lowe, and B.M. Wetherbee. 1993. Movements, distribution

- and growth rates of the white goatfish, *Mulloides flavolineatus* in a fisheries conservation zone. *Bull. Mar. Sci.* 52(3): 982-992.
- Holmes, E.E., M.A. Lewis, J.E. Banks, and R.R. Veit. 1994. Partial differential equations in ecology: spatial interactions and population dynamics. *Ecology*. 75(1): 17-29.
- Hourigan, T.F. 1986. An experimental removal of a territorial pomacentrid: effects on the occurrence and behavior of competitors. *Environmental Biology of Fishes*. 15(3): 161-169.
- Huitema, B.E. 1980. *The Analysis of Covariance and Alternatives*. John Wiley and Sons, New York. U.S.A.
- Humann, P. 1996. *Reef Fish Identification: Florida Caribbean Bahamas*. New World Publications.
- Hunt, P.C., and J.W. Jones. 1974. A population study of *Barbus barbus* (L.) in the River Severn, England. II. Movements. *J. of Fish Biol.* 44: 11-22.
- Huntingford, F.A. 1992. Development of behaviour in fish. Pp. 57-80. In: T.J. Pitcher (ed.) *Behaviour of Teleost Fishes*. Chapman and Hall, London.
- Huntsman, G. R. 1979. Predation's role in structuring reef fish communities. In R. H. Stroud and H. Clepper (eds.) *Predator-prey systems in fisheries management*. Sport Fishing Institute, Washington, D.C. 103-108.
- Hutchinson, G. E. 1957. Concluding remarks. *Cold Spring Harbour Symposium on Quantitative Biology*. 22: 415-427.
- Hyndes, G.A., Platell, M.E., and I.C. Potter. 1997. Relationships between diet and body size, mouth morphology, habitat and movements of six sillaginid species in coastal waters: Implications for resource partitioning. *Mar. Biol. Berlin*. 128 (4): 585-598.
- Inouye, B.D. 1999. Integrating nested spatial scales: implications for the coexistence of competitors on a patchy resource. *J. Anim. Ecol.* 68: 150-162.
- Itzkowitz, M. 1977a. Spatial organization of the Jamaican damselfish community. *J. Exp. Mar. Biol. Ecol.* 28: 217-241.
- Itzkowitz, M. 1977b. Social dynamics of mixed-species groups of Jamaican reef fishes. *Behav. Ecol. Sociobiol.* 2: 361-384.
- Itzkowitz, M. 1985. Aspects of the population dynamics and reproductive success in the permanently territorial beaugregory damselfish. *Mar. Behav. Physiol.* 12: 57-69.
- Itzkowitz, M. 1990. Heterospecific intruders, territorial defense and reproductive success in the beaugregory damselfish. *J. Exp. Mar. Biol. Ecol.* 140: 49-59.

- Ives, A.R. 1988. Aggregation and the coexistence of competitors. *Annales Zoologica Fennici*. 25: 75-88.
- Ives, A.R., and R.M. May. 1985. Competition within and between species in a patchy environment: relations between microscopic and macroscopic models. *J. Theor. Biol.* 115: 65-92.
- Jennings, S., D.P. Boule, N.V.C. Polunin. 1996. Habitat correlates of the distribution and biomass of Seychelle's reef fishes. *Env. Biol. Fish.* 46: 15-25.
- Jennrich, R.I., and F.B. Turner. 1969. Measurement of non-circular home range. *J. Theor. Biol.* 22: 227-237.
- Jepsen, N., A. Koed, and F. Okland. 1999. The movements of pikeperch in a shallow reservoir. *J. Fish Biol.* 54: 1083-1093.
- Jones, G.P. 1980. Growth and reproduction in the protogynous hermaphrodite, *Pseudolabrus celidotus* (Pisces: Labridae), in New Zealand. *Copeia*. 1980: 660-675.
- Jones, G.P. 1984a. The influence of habitat and behavioural interactions on the local distribution of the wrasse, *Pseudolabrus celidotus*. *Env. Biol. Fish.* 10(1/2): 43-58.
- Jones, G.P. 1984b. Population ecology of the temperate reef fish *Pseudolabrus celidotus* Bloch and Schneider (Pisces: Labridae). I. Factors influencing recruitment. *J. Exp. Mar. Biol. Ecol.* 75: 257-276.
- Jones, G.P. 1986. Food availability affects growth in a coral reef fish. *Oecologia*. 70:136-139
- Jones, G.P. 1987. Competitive interactions among adults and juveniles in a coral reef fish. *Ecology*. 68(5): 1534-1547.
- Jones, G.P. 1988a. Ecology of rocky reef fish of north-eastern New Zealand. *N.Z.J. Mar. Freshwater Res.* 22: 445-462.
- Jones, G.P. 1988b. Experimental evaluation of the effects of habitat-structure and competitive interactions on the juveniles of two coral reef fishes. *J. Exp. Mar. Biol. Ecol.* 123: 115-126.
- Jones, G.P. 1990. The importance of recruitment to the dynamics of a coral reef fish population. *Ecology*. 71: 1691-1698.
- Jones, G.P. 1991. Postrecruitment processes in the ecology of coral reef fish populations: a multifactorial perspective. *In: The Ecology of Fishes on Coral Reefs* (ed. P.F. Sale) pp. 294-328. Academic Press, San Diego.
- Jones, G.P., and U.L. Kaly. 1995. Criteria for selecting marine organisms in biomonitoring

- studies. In: *Detection of Ecological Impacts: Conceptual Issues and Application in Coastal Marine Habitats* (eds. R.J. Schmitt and C.W. Osenberg). 39-56. University of California Press, San Diego.
- Jones, G.P., and C. Syms. 1998. Disturbance, habitat structure, and the ecology of fishes on coral reefs. *Aust. J. Ecol.* 23: 287-297.
- Jones, K.M.M. and E.G. Boulding. 1999. State-dependent habitat selection by an intertidal snail the costs of selecting a physically stressful microhabitat. *J. Exp. Mar. Biol. Ecol.* 242:149-177.
- Jongman, R.H.G., C.J.F. ter Braak, and O.F.R. van Tongeren (eds.) 1987. *Data analysis on community and landscape ecology*. Pudoc. Wageningen. 298pp.
- Katzir, G. 1981. Aggression by the damselfish *Dascyllus aruanus* L. towards conspecifics and heterospecifics. *Anim. Behav.* 29:835-841.
- Keast, A., and D. Webb. 1966. Mouth and body form relative to feeding ecology in the fish fauna of a small lake, Lake Opinicon, Ontario. *J. Fish. Res. Bd. Canada.* 23(12):1845-1874.
- Keast, A. 1977. Mechanisms expanding niche width and minimizing intraspecific competition in two centrarchid fishes. *Evol. Biol.* 10: 333-395.
- Keast, A. 1978. Feeding interrelations between age-groups of pumpkinseed *Lepomis gibbosus* and comparisons with bluegill (*L. macrochirus*). *J. Fish. Res. Bd. Can.* 35: 12-27.
- Keenleyside, M.H.A. 1972. The behaviour of *Abudefduf zonatus* (Pisces, Pomacentridae) at Heron Island, Great Barrier Reef. *Anim. Behav.* 20: 763-774.
- Kennedy, G.J.A. 1981. Individual variation in homing tendency in the European minnow, *Phoxinus phoxinus* (L.). *Anim. Behav.* 29: 621-625.
- Kie, J.G., Baldwin, J.A., and C.J. Evans. 1994. CALHOME: Home Range Analysis Program. <http://nhsbig.inhs.uiuc.edu>, 03/03/99
- Kramer, D.L., and M.R. Chapman. 1999. Implications of fish home range size and relocation for marine reserve function. *Env. Biol. Fish.* 55: 65-79.
- Krebs, C.J. 1995. *Ecology: The Experimental Analysis of Distribution and Abundance*. Harper Collins. U.S.A.
- Krebs, J.R., and N.B. Davies. 1987. *An introduction to behavioural ecology*. 2nd Edition. Blackwell Scientific Publ. Oxford. 389pp.
- L'Abée Lund, J.H., A. Langeland, B. Jonsson, and O. Ugedal. 1993. Spatial segregation by age and size in Arctic charr: A trade-off between feeding possibility and risk of predation. *J. Animal Ecology.* 62(1): 160-168.

- Larson, R.J. 1980. Territorial behavior of the black and yellow rockfish and gopher rockfish (Scorpaenidae, Sebastes). *Mar. Biol.* 58: 111-122.
- Lawson, G.L., D.L. Kramer, and W. Hunte. 1999. Size-related habitat use and schooling behaviour in two species of surgeonfish (*Acanthurus bahianus* and *A. coeruleus*) on a fringing reef in Barbados, West Indies. *Env. Biol. Fish.* 54: 19-33.
- Lejeune, P. 1987. The effect of local density on social behavior and sex change in the Mediterranean labrid *Coris julis*. *Env. Biol. Fish.* 18(2): 135-141.
- Lemmens, E.H.R., W.L.T. van Densen, and R. Knijn. 1990. The fish community structure in Tjeukemeer in relation to fishery habitat utilization. *J. Fish Biol.* 36:933-945.
- Levin, P. S. 1993. Habitat structure, conspecific presence and spatial variation in the recruitment of a temperate reef fish. *Oecologia.* 94:176-185.
- Lirman, D. 1994. Ontogenetic shifts in habitat preferences in the three-spot damselfish, *Stegastes planifrons* (Cuvier), in Roatan Island, Honduras. *J. Exp. Mar. Biol. Ecol.* 180(1): 71-81.
- Lockett, M.M., Suthers, I.M. 1998. Ontogenetic diet shift and feeding activity in the temperate reef fish *Cheilodactylus fuscus*. *Proc. Linn. Soc. New South Wales.* 120 (0): 105-116.
- Lomnicki, A. 1999. Individual-based models and the individual-based approach to population ecology. *Ecol. Model.* 115: 191-198.
- Love, M.S., and A. W. Ebeling. 1978. Food and habitat of three switch-feeding fishes in the kelp forests off Santa Barbara, California. *U.S. Fish. Bull.* 76:257-271.
- Low, R.M. 1971. Interspecific territoriality in a pomacentrid reef fish, *Pomacentrus flavicauda* Whitley. *Ecology.* 52: 649-654.
- Lowe, C.G., B.M. Wetherbee, G.L. Crow., and A.L. Tester. 1996. Ontogenetic dietary shifts and feeding behavior of the tiger shark, *Galeocerdo cuvier*, in Hawaiian waters. *Env. Biol. Fish.* 47(2): 203-211.
- Lowry, M.B., and I.M. Suthers. 1998. Home range, activity and distribution patterns of a temperate rocky-reef fish, *Cheilodactylus fuscus*. *Mar. Biol.* 132: 569-578.
- Luckhurst, B.E. and K. Luckhurst. 1978. Diurnal space utilization in coral reef fish communities. *Mar. Biol. (Berl.)* 49: 325-332.
- MacArthur, R., and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. *Am. Nat.* 101:377-385.
- Macpherson, E. 1994. Substrate utilization in a Mediterranean littoral fish community. *Mar. Ecol. Prog. Ser.* 114:211-218.

- Magurran, A.E. 1990. The adaptive significance of schooling as an antipredator defence in fish. *Ann. Zool. Fenn.* 27:51-66.
- Magurran, A.E., and B.H. Seghers. 1990. Risk sensitive courtship in the guppy (*Poecilia reticulata*). *Behaviour.* 112: 194-201.
- Maher, C.R. and D.F. Lott. 1995. Definitions of territoriality used in the study of variation in vertebrate spacing systems. *Anim. Behav.* 49: 1581-1597.
- Malmquist, H.J., S.S. Snorrason, S. Skulason, B. Jonsson, O.T. Sandlund, and P.M. Jonasson. 1992. Diet differentiation in polymorphic Arctic charr in Thingvallavatn, Iceland. *J. Anim. Ecol.* 61: 21-35.
- Manly, B.F.J., L.L. McDonald, and D.L. Thomas. 1993. Resource selection by animals. Chapman and Hall, London, U.K.
- Martin, J., and A. Salvador. 1995. Microhabitat selection by the Iberian rock lizard *Lacerta monticola*: effects on density and spatial distribution of individuals. *Biol. Cons.* 79: 303-307.
- Marvin, G.A. 1998. Territorial behavior of the plethodontid salamander *Plethodon kentucki*: influence of habitat structure and population density. *Oecologia.* 114: 133-144.
- Matthews, W.J. 1998. Patterns in freshwater fish ecology. Chapman and Hall. U.S.A.
- Matsumoto, K., M. Kohda, Y. Yanagisawa. 1999. Size-dependent feeding association of two wrasses (genus *Pseudolabrus*) with the morwong, *Goniistius zonatus*. *Ichthyol. Res.* 46(1): 57-65.
- Matthews, W.J. 1998. Structure of fish assemblages. Ch. 2 In: *Patterns in Freshwater Fish Ecology*. Chapman and Hall. Mass. U.S.A. pp. 30-85.
- McAffe, S.T., and S.G. Morgan. 1996. Resource use by five sympatric parrotfishes in the San Blas Archipelago, Panama. *Marine Biology.* 125: 427-437.
- McCarthy, M.A. 1999. Effects of competition on natal dispersal distance. *Ecol. Model.* 114: 305-310.
- McCormick, M.I. 1994. Comparison of field methods for measuring surface topography and their associations with a tropical reef fish assemblage. *Mar. Ecol. Prog. Ser.* 112:87-94.
- McFarland, W.N. 1979. Observations on recruitment in haemulid fishes. *Pro. Gulf. Caribb. Fish. Inst.* 32:132-138.
- McGehee, M.A. 1995. Juvenile settlement, survivorship, and *in situ* growth rates of four species of Caribbean damselfishes in the genus *Stegastes*. *Env. Biol. Fish.* 44: 393-401.

- McNab, B.K. 1963. Bioenergetics and the determination of home range size. *Am. Nat.* 97(894): 133-140.
- Meekan, M.G. 1988. Settlement and mortality patterns of juvenile reef fishes at Lizard Island Northern Great Barrier Reef. *Proc. 6th Int. Coral Reef. Symp.* 2: 779-784.
- Meekan, M.G., A.D.L. Steven and M.J. Fortin. 1995. Spatial patterns in the distribution of damselfishes on a fringing coral reef. *Coral Reefs* 14: 151-161.
- Melville, J. and R. Swain. 1999. Home-range characteristics of an alpine lizard, *Niveoscincus microlepidotus* (Scincidae), on Mt. Wellington, southern Tasmania. *Wildlife Res.* 26: 263-270.
- Menge, B.A. and A. M. Olson. 1990. Role of scale and environmental factors in regulation of community structure. *TREE* 5(2): 52-57.
- Miller, R.J. 1978. Agonistic behavior in fishes and terrestrial vertebrates. Ch. 10. *In: Contrasts in behavior: Adaptations in the Aquatic and Terrestrial Environments.* Eds. E.S. Reese, and F.J. Lighter. John Wiley and Sons, New York, U.S.A.
- Minns, C.K. 1995. Allometry of home range size in lake and river fishes. *Can. J. Fish. Aquat. Sci.* 52: 1499-1508.
- Mittelbach, G. 1986. Predator-mediated habitat use: some consequences for species interactions. *Env. Biol. Fish.* 16: 1-3.
- Mittelbach, G.G. and C.W. Osenberg. 1993. Stage-structured interactions in bluegill: consequences of adult resource variation. *Ecology.* 74 (8): 2381-2394.
- MOCHA Image Analysis Software. 1993. Jandel Scientific. San Rafael, California, U.S.A.
- Mohr, C.O. 1947. Table of equivalent populations of North American mammals. *Amer. Midl. Nat.* 37: 223-249.
- Moller, A.P. 1991. Clutch size, nest predation, and distribution of avian unequal competitors in a patchy environment. *Ecology.* 72:1336-1349.
- Molls, F. 1999. New insights into the migration and habitat use by bream and white bream in the floodplain of the River Rhine. *J. Fish. Biol.* 55(6): 1187-1200.
- Molofsky, J. 1994. Population dynamics and pattern formation in theoretical populations. *Ecology.* 75(1): 30-39.
- Montgomery, W.L. 1980. Comparative feeding ecology of two herbivorous damselfishes (Pomacentridae: Teleostei) from the Gulf of California, Mexico. *J. exp. Mar. Biol. Ecol.* 47: 9-24.

- Morrison, M.L., B.G. Marcot, and R.W. Mannan. 1992. Wildlife-habitat relationships. The University of Wisconsin Press, U.S.A.
- Morse, D.H. 1977. Feeding behavior and predator avoidance in heterospecific groups. *Biol. Science*. 124: 863-886.
- Muller, K.L. 1998. The role of conspecifics in habitat settlement in a territorial grasshopper. *Animal Behaviour*. 56: 479-485.
- Munday, P.L., and S.K. Wilson. 1997. Comparative efficacy of clove oil and other chemicals in anaesthetization of *Pomacentrus amboinensis*, a coral reef fish. *Journal of Fish Biology*. 51: 931-938.
- Muñoz, A.A. and F.P. Ojeda. 1998. Guild structure of carnivorous intertidal fishes of the Chilean coast: implications of ontogenetic dietary shifts. *Oecologia*. 114: 563-573.
- Myrberg, A.A. Jr., and R.E. Thresher. 1974. Interspecific aggression and its relevance to the concept of territoriality in reef fishes. *Am. Zool.* 14: 81-96.
- Nagelkerken, W. 1977. The distribution of the graysby *Petrometopon cruentatum* (Lacepede) on the coral reef at the southwest coast of Curacao. *Proc. Of the 3rd Int. Coral Reef Symp.*, Miami 1: 311-315.
- Nemtzov, S.C. 1997. Intraspecific variation in home range exclusivity by female green razorfish, *Xyrichtys splendens* (family Labridae), in different habitats. *Env. Biol. Fish.* 50: 371-381.
- Norman, M.D., and G.P. Jones. 1984. Determinants of territory size in the pomacentrid reef fish, *Parma victoriae*. *Oecologia*. 61: 60-69.
- Nursall, J.R. 1974. Some territorial behavioral attributes of the surgeonfish *Acanthurus lineatus* at Heron Island, Queensland. *Copeia*. 1974(4): 950- 149.
- Nursall, J.R. 1977. Territoriality in the red lip blennies (*Ophioblennius atlanticus* - Pisces: Blenniidae). *J.Zool., Lond.* 182: 205-223.
- Odum, E.P. 1975. Ecology: the link between the natural and the social sciences. Holt, Rinehart and Winston, N.Y. 244pp.
- Ogden, J.C., and N.S. Buckman. 1973. Movements, foraging groups, and diurnal migrations of the striped parrotfish *Scarus croicensis* Bloch (Scaridae). *Ecology*. 54: 589-596.
- Ogden, J.C., and P.R. Ehrlich. 1977. The behavior of heterotypic resting schools of juvenile grunts (Pomadasyidae). *Mar. Biol.* (1977):273-280.
- Orians, G.H. 1961. Social stimulation within blackbird colonies. *Condor*. 63: 330-337.

- Ormond, R.F.G. 1980. Aggressive mimicry and interspecific feeding associations among Red Sea coral reef predators. *J. Zool. Lond.* 191: 247-262.
- Osburn, J. 1972. On the biology of *Ophioblennius atlanticus* (abstract). *Atoll Res. Bull.* No. 152:6.
- Overholtzer, K.L., and P.J. Motta. 1999. Comparative resource use by juvenile parrotfishes in the Florida Keys. *Mar. Ecol. Prog. Ser.* 177: 177-187.
- Parkinson, D., J.C. Philippart, and E. Baras. 1999. A preliminary investigation of spawning migrations of grayling in a small stream as determined by radio-tracking.
- Parrish, J.D. 1987. Characteristics of fish communities on coral reefs and in potentially interacting shallow habitats in tropical oceans of the world. *UNESCO Rep. Mar. Sci.* 46:171-218.
- Peters, R.H. 1976. Tautology in evolution and ecology. *Am. Nat.* 110:1-12.
- Petersen, C.W. 1991. Variation in fertilization rate in the tropical reef fish, *Halichoeres bivittatus*: correlates and implications. *Biol. Bull.* 181: 232-237.
- Platell, M.E., and I.C. Potter. 1999. Partitioning of habitat and prey by abundant and similar-sized species of the Triglidae and Pempherididae (Teleostei) in coastal waters. *Est. Coast. Shelf. Sci.* 48(2): 235-252.
- Poling, K.R., and L.A. Fuiman. 1997. Sensory development and concurrent behavioural changes in Atlantic croaker larvae. *J. Fish Biol.* 51(2): 402-421.
- Pottle, R.A. and J.M. Green. 1979. Territorial behaviour of the north temperate labrid, *Tautoglabrus adspersus*. *Can. J. Zool.* 57: 2337-2347.
- Pulliam, H.R., and T. Caraco. 1984. Living in groups: is there an optimal group size? Pp. 122-147. In: J.R. Krebs & N.B. Davies (ed.) *Behavioural Ecology: An evolutionary approach*. Blackwell, Oxford.
- Randall, J.E. 1967. Food habits of reef fishes of the West Indies. *Stud. Trop. Oceanogr.* 5: 665-847.
- Randall, J.E., and J.E. Bohlke. 1965. Review of the Atlantic Labrid fishes of the Genus *Halichoeres*. *Proc. Acad. Nat. Sci.* 15: 896-941.
- Reese, E.S. 1973. Duration of residence by coral reef fishes on "home" reefs. *Copeia*. 1973(1): 145-149.
- Reese, E.S. 1978. The study of space-related behavior in aquatic animals: special problems and selected examples. In: *Contrasts in Behaviour: Adaptations in the Aquatic and Terrestrial Environments*. Eds. E.Reese and F.J. Lighter. Pp. 347-374. Wiley Interscience: New York.

- Reinboth, R. 1973. Dualistic reproductive behavior in the protogynous wrasse, *Thalassoma bifasciatum* and some observations on its day-night changeover. *Helgolander wiss. Meeresunters.* 24: 174-191.
- Resetaits, W.J., Jr. 1995. Limiting similarity and the intensity of competitive effects on the mottled sculpin, *Cottus bairdi*, in experimental stream communities. *Oecologia.* 104:31-38.
- Richmond, A.M., and B. Kynard. 1995. Ontogenetic behavior of shortnose sturgeon *Acipenser brevirostrum*. *Copeia.* 1995(1): 172-182.
- Risk, A. 1998. The effects of interactions with reef residents on the settlement and subsequent persistence of ocean surgeonfish, *Acanthurus bahianus*. *Env. Biol. Fish.* 51: 377-389.
- Risk, M.J. 1972. Fish diversity on a coral reef in the Virgin Islands. *Atoll. Res. Bull.* 153: 1-6.
- Roberts, C.M., and R.F.G. Ormond. 1987. Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. *Mar. Ecol. Prog. Ser.* 41: 1-8.
- Roberts, C.M., R.F.G. Ormond, and A.R.D. Shepherd. 1988. The usefulness of butterflyfishes as environmental indicators on coral reefs. *Proc. 6th Int. Coral Reef Symp.* 2: 331-336.
- Robertson, D.R. 1981. The social and mating systems of two labrid fishes, *Halichoeres maculipinna* and *H. garnoti*, off the Caribbean Coast of Panama. *Mar. Biol.* 64: 327-340.
- Robertson, D.R. 1988. Abundances of surgeonfishes on patch-reefs in Caribbean Panama: due to settlement, or post-recruitment events? *Mar. Biol.* 97: 495-501.
- Robertson, D.R. 1996. Interspecific competition controls abundance and habitat use of territorial Caribbean damselfishes. *Ecology.* 77(3): 885-599.
- Robertson, D.R., and S. D. Gaines. 1986. Interference competition structures habitat use in a local assemblage of coral reef fishes. *Ecology* 67(5), 1372-1383.
- Robertson, D.R. and S.G. Hoffman. 1977. The roles of female mate choice and predation in the mating system of some tropical labroid fishes. *Z. Tierpsychol.* 45: 298-320.
- Robertson, D.R. and B. Lassig. 1980. Spatial distribution patterns and coexistence of a group of territorial damselfish from the Great Barrier Reef. *Bulletin of Marine Science.* 30: 187-203.
- Robertson, D.R., and J.M. Sheldon. 1979. Comparative interactions and the availability of sleeping sites for a diurnal coral reef fish. *J. Exp. Mar. Biol. Ecol.* 40:285-298.
- Robertson, D.R., H.P.A. Sweatman, E.A. Fletcher, and M.G. Cleland. 1976. Schooling as a mechanism for circumventing the territoriality of competitors. *Ecology.* 57: 1208-1220.

- Rodenhouse, N.L., T.W. Sherry, and R.T. Holmes. 1997. Site-dependent regulation of population size: a new synthesis. *Ecology*. 78(7): 2025-2042.
- Roede, M.J. 1972. Color as related to size, sex, and behavior in seven Caribbean Labrid Fish Species (Genera *Thalassoma*, *Halichoeres*, *Hemipteronotus*). *Studies on the Fauna of Curacao and Other Caribbean Islands*. 138: 1-264.
- Rolando, A. 1998. Factors affecting movements and home ranges in the jay (*Garrulus glandarius*). *J. Zool. Lond.* 246: 249-257.
- Rooney, S.M., A. Wolfe, and T.J. Hayden. 1998. Autocorrelated data in telemetry studies: time to independence and the problem of behavioural effects. *Mammal Review*. 28(2): 89-98.
- Rosenzweig, M.L., and Z. Abramsky. 1986. Centrifugal community organization. *Oikos*. 46: 339-348.
- Ross, S.T. 1986. Resource partitioning in fish assemblages: a review of field studies. *Copeia*. 1986(2): 352-388.
- Russ, G. 1984. Distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef. I. Levels of variability across the entire continental shelf. *Mar. Ecol. Prog. Ser.* 20: 23-34.
- Russell, B.C., F.H. Talbot, S.B. Domm. 1974. Patterns of colonization of artificial reefs by coral reef fishes. *Proc. Int. Symp. Coral Reefs*. 2nd. 1:207-215.
- Saab, V. 1999. Importance of spatial scale to habitat use by breeding birds in riparian forests: a hierarchical analysis. *Ecological Applications*. 9(1): 135-151.
- Sakakura, Y., and K. Tsukamoto. 1999. Ontogeny of aggressive behaviour in schools of yellowtail, *Seriola quinqueradiata*. *Env. Biol. Fish.* 56(1-2): 231-242.
- Sale, P.F. 1968. Influence of cover availability on depth preference of the juvenile manini, *Acanthurus triostegus sandvicensis*. *Copeia*. 4:802-807.
- Sale, P.F. 1971. Extremely limited home range in a coral reef fish, *Dascyllus aruanus* (Pisces: Pomacentridae). *Copeia*. 1971(2): 324-327.
- Sale, P.F. 1974. Mechanisms of coexistence in a guild of territorial fishes at Heron Island. *Proc. Second. Int. Symp. Coral Reefs*. 1: 193-206
- Sale, P.F. 1977. Maintenance of high diversity in coral reef fish communities. *Am. Nat.* 111: 337-359.
- Sale, P.F. 1978a. Reef fishes and other vertebrates: a comparison of social structures. Ch. 11. In: *Contrasts in Behavior: Adaptations in the Aquatic and Terrestrial Environments*. Eds.

- E.S. Reese and F.J. Lighter. John Wiley and Sons. New York. 406pp.
- Sale, P.F. 1978b. Coexistence of coral reef fishes - a lottery for living space. *Env. Biol. Fish.* 3: 85-102.
- Sale, P.F. 1980. The ecology of fishes on coral reefs. *Oceanogr. Mar. Biol. Ann. Rev.* 18: 367-421.
- Sale, P.F. 1991a. Habitat structure and recruitment in coral reef fishes. Ch. 10. *In*: S.S. Bell, E.D. McCoy, and H.R. Mushinsky (eds.). *Habitat Structure: The physical arrangement of objects in space*. Chapman and Hall. London. Pp. 197-210.
- Sale, P.F. (ed.) 1991b. *The Ecology of Fishes on Coral Reefs*. Academic Press, San Diego.
- Sale, P.F., Doherty, P.J., G.J. Eckert, W.A. Douglas, and D.J. Ferrell. 1984. Large scale spatial and temporal variation in recruitment to fish populations on coral reefs. *Oecologia*. 64: 191-198.
- Sale, P.F. and W.A. Douglas. 1984. Temporal variability in the community structure of fish on coral patch reefs and the relation of community structure to reef structure. *Ecology*. 65: 409-422.
- Sale, P.F., and J.A. Guy. 1992. Persistence of community structure: what happens when you change taxonomic scale? *Coral Reefs*. 11: 147-154.
- Sale, P.F., J.A. Guy, and W.J. Steel. 1994. Ecological structure of assemblages of coral reef fishes on isolated patch reefs. *Oecologia* 98:83-99.
- Samoilys, M.A. 1997. Movement in a large predatory fish: coral trout, *Plectropomus leopardus* (Pisces: Serranidae), on Heron Reef, Australia. *Coral Reefs*. 16: 151-158.
- Santiago, J.A., and J.J. Castro. 1997. Acoustic behaviour of *Abudefduf luridis*. *J. of Fish Biol.* 51: 952-959.
- Sayer, M.D.J., R.N. Gibson, and R.J.A. Atkinson. 1993. Distribution and density of populations of goldsinny wrasse (*Ctenolabrus rupestris*) on the west coast of Scotland. *J. Fish. Biol.* 43(a): 157-167.
- Schmitt, R.J., and S.J. Holbrook. 1985. Patch selection by juvenile black surfperch (Embiotocidae) under variable risk: Interactive influence of food quality and structural complexity. *J. Exp. Mar. Biol. Ecol.* 85: 269-285.
- Schmitt, R.J., and S. J. Holbrook. 1996. Local-scale patterns in a planktivorous damselfish- do they predict recruitment? *Mar. Freshwater Res.* 47:449-63.
- Schoener, T.W. 1968. Sizes of feeding territories among birds. *Ecology*. 49: 123-141.

- Schoener, T.W. 1983. Field experiments on interspecific competition. *Am. Nat.* 122(2): 240-285.
- Schoener, T.W. and A. Schoener. 1982. Intraspecific variation in home-range size in some *Anolis* lizards. *Ecology*. 63: 809-823.
- Seastedt, T.R., and S.F. MacLean. 1979. Territory size and composition in relation to resource abundance in Lapland longspurs breeding in arctic Alaska. *Auk*. 96: 131-142.
- Setran, A.C., and D.W. Behrens. 1993. Transitional ecological requirements for early juveniles of two sympatric stichaeid fishes, *Cebidichthys violaceus* and *Xiphister mucosus*. *Env. Biol. Fish.* 37(4): 381-195.
- Shapiro, D.Y. 1987. Patterns of space use common to widely different types of social groupings of a coral reef fish. *Env. Biol. Fish.* 18(3): 183-194.
- Shapiro, D.Y., G. Garcia-Moliner, and Y. Sadovy. 1994. Social system of an inshore stock of the red hind grouper, *Epinephelus guttatus* (Pisces: Serranidae). *Env. Biol. Fish.* 41: 415-422.
- Shibuno, R., H. Hashimoto, K. Gushima. 1994. Changes with growth in feeding habits and gravel turning behavior of the wrasse, *Coris gaimard*. *Japanese Journal of Ichthyology*. 41(3): 301-306.
- Shields, W.M., J.R. Crook, M.L. Hebblethwaite, and S.S. Wiles-Ehmann. 1988. Ideal free coloniality in the swallows. In: *Ecology of Social Behavior* (Ed. By C.N. Slobodchikoff), pp. 189-228. San Diego, California: Academic Press.
- Shulman, M.J. 1984. Resource limitation and recruitment patterns in a coral reef fish assemblage. *J. Exp. Mar. Biol. Ecol.* 74: 85-109.
- Shulman, M.J. 1985a. Recruitment coral reef fishes: effects of distribution of predators and shelter. *Ecology*. 66(3):1056-1066.
- Shulman, M.J. 1985b. Coral reef fish assemblages: intra- and interspecific competition for shelter sites. *Env. Biol. Fish.* 13: 81-92.
- Shulman, M.J., and J.C. Ogden. 1987. What controls tropical reef fish populations: recruitment or benthic mortality? An example in the Caribbean reef fish *Haemulon flavolineatum*. *Mar. Ecol. Prog. Ser.* 39: 233-242.
- SigmaStat: Statistical Software. 1997. Version 2.0. SPSS Inc.; Chicago, Ill., U.S.A.
- Sikkel, P.C. 1990. Social organization and spawning in the Atlantic sharpnose puffer, *Canthigaster rostrata* (Tetraodontidae). *Env. Biol. Fish.* 27: 243-254.
- Sikkel, P.C., and P.D. Hardison. 1992. Interspecific feeding associations between the goatfish *Mulloidides martinicus* (Mullidae) and a possible aggressive mimic, the snapper, *Ocyurus*

- chrysurus* (Lutjanidae). *Copeia*. 1992: 914-917.
- Simon, C.A. 1975. The influence of food abundance on territory size in the iguanid lizard *Sceloporus jarrovi*. *Ecology*. 56: 993-998.
- Skulason, S., and T.B. Smith. 1995. Resource polymorphisms in vertebrates. *TREE*. 10(9): 366-370.
- Slatkin, M., and D.J. Anderson. 1984. A model of competition for space. *Ecology*. 65: 1840-1845.
- Sluka, R.S., and K.M. Sullivan. 1996. The influence of habitat on the size and distribution of groupers in the upper Florida Keys. *Env. Biol. Fish.* 47:177-189.
- Smith, C.L. 1978. Coral reef fish communities: A compromise view. *Env. Biol. Fish.* 3: 109-128.
- Smith, C.L. and J.C. Tyler. 1972. Space resource sharing in a coral reef fish community. Results of the Tektite Program. *Bulletin of the Natural History Museum of L.A. County*, 14, 12-170.
- Smith, C.L. and J.C. Tyler. 1973a. Population ecology of a Bahamian suprabenthic shore fish assemblage. *Am. Mus. Novitates*. 2528: 1-38.
- Smith, C.L. and J.C. Tyler. 1973b. Direct observations of resource sharing in coral reef fish. *Helgol. Wiss. Meeresunter.* 24: 264-275.
- Smith, C.L. and J.C. Tyler. 1975. Succession and stability in fish communities of the dome-shaped patch reefs in the West Indies. *Am. Mus. Novit.* 2572: 1-18.
- Sogard, S.M., G.V.N. Powell, and J.G. Holmquist. 1989. Spatial distribution and trends in abundance of fishes residing in seagrass meadows on Florida mudbanks. *Bull. Mar. Sci.* 44: 179-199.
- Sousa, W.P. 1984. Intertidal mosaics: patch size, propagule availability and spatially variable patterns of succession. *Ecology* 65:1918-1935.
- Southern, H.N., and R.W. Lowe. 1968. The pattern and distribution of prey and predation in Tawny Owl territories. *J. Anim. Ecol.* 37: 75-97.
- Springer, V.G., and A.J. McErlean. 1962. A study of the behaviour of some tagged south Florida reef fishes. *Am. Midl. Nat.* 67: 386-397.
- Stamps, J.A. 1987. Conspecifics as cues to territory quality: a preference of juvenile lizards (*Anolis aeneus*) for previously used territories. *American Naturalist*. 129: 629-642.
- Stamps, J.A. and M. Buechner. 1985. The territorial defense hypothesis and the ecology of insular vertebrates. *Quart. Rev. Biol.* 60(2): 155-181.

- Stamps, J.A., M. Buechner, and V.V. Krishnan. 1987. The effects of habitat geometry on territorial defense costs: intruder pressure in bounded habitats. *Amer. Zool.* 27: 307-325.
- Stamps, J.A. and P.K. Eason. 1989. Relationships between spacing behavior and growth rates: a field study of lizard feeding territories. *Behav. Ecol. Sociobiol.* 25:99-107.
- Statistica® '98 Edition. Kernel Release 5.1. StatSoft, Inc. U.S.A.
- Stein, S.L., B.N. Tissot, M.A. Hixon, and W. Barss. 1992. Fish-habitat associations on a deep reef at the edge of the Oregon continental shelf. U.S. National Marine Fisheries Service Fishery Bulletin. 90 (3): 540-551.
- Stephens, J.S., and K.E. Zerba. 1981. Factors affecting fish diversity on a temperate reef. *Env. Biol. Fish.* 6: 111-121.
- Stoner, A.W. 1983. Distribution of fishes in seagrass meadows: role of macrophyte biomass and species composition. *Fish. Bull. U.S.* 81: 837-846.
- Stott, B. 1967. The movements and population densities of roach (*Rutilus rutilus* L.) and gudgeon (*Gobio gobio*, L.) in the River Mole. *J. of Anim. Ecol.* 36: 407-423.
- Sugihara, G. 1980. Minimal community structure: an explanation of species abundance patterns. *Am. Nat.* 116(6): 770-787.
- Syms, C. 1998. Disturbance and the structure of coral reef fish communities on the reef slope. *J. Exp. Mar. Biol. Ecol.* 230: 151-167.
- SYSTAT version 8.0 standard version. 1998. Copyright SPSS Inc.
- Szedlmayer, S.T. 1997. Ultrasonic telemetry of red snapper, *Lutjanus campechanus*, at artificial reef sites in the northeast Gulf of Mexico. *Copeia*. 4: 846-850.
- Szedlmayer, S.T., and R.L. Shipp. 1994. Movement and growth of red snapper, *Lutjanus campechanus*, from an artificial reef area in the northeastern Gulf of Mexico. *Bull. Mar. Sci.* 55: 887-896.
- Tabachnik, B.G. and L.S. Fidell. 1989. Using multivariate statistics, second edition. HarperCollins Publishers, Inc. New York. 746pp.
- Tabor, R.A. and W. A. Wurtsbaugh. 1991. Predation risk and the importance of cover for juvenile rainbow trout in lentic systems. *Trans. Amer. Fish. Soc.* 120:728-738.
- Taylor, C.M. 1996. Abundance and distribution within a guild of benthic stream fishes: local processes and regional patterns. *Freshwater Biology.* 36: 385-39
- Tejerina-Garro, F., R. Fortin, and M.A. Rodriguez. 1998. Fish community structure in relation to environmental variation in floodplain lakes of the Araguaia River, Amazon Basin. *Env.*

Biol. Fish. 51: 399-410.

- terBraak, C.J.F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology*. 67: 1167-1179.
- Thibault, A. and J. Bovet. 1999. Homing strategy of the Eastern Chipmunk, *Tamias striatus* (Mammalia: Rodentia): Validation of the critical distance model. *Ethology*. 105: 73-82.
- Thompson, S. 1983. Homing in a territorial reef fish. *Copeia*. 1983(3): 932-934.
- Thresher, R.E. 1976. Field experiments on species recognition by the threespot damselfish, *Eupomacentrus planifrons* (Pisces: Pomacentridae). *Anim. Behav.* 24: 562-569.
- Thresher, R.E. 1977. Ecological determinants of social organization of reef fishes. In: Proc. 3rd Int. Coral Reef Symposium. 551-557.
- Thresher, R.E. 1979. Social behavior and ecology of two sympatric wrasses (Labridae: *Halichoeres* spp.) off the coast of Florida. *Mar. Biol.* 53: 161-172.
- Thresher, R.E. 1984. Reproduction in reef fishes. T.F.H. Publications, Neptune City. 399pp.
- Tilman, D. 1994. Competition and biodiversity in spatially-structured habitats. *Ecology*. 75(1): 2-16.
- Tolimieri, N. 1998. Effects of substrata, resident conspecifics and damselfish on the settlement and recruitment of the stoplight parrotfish, *Sparisoma viride*. *Env. Biol. Fish.* 53:393-404.
- Tribble, G.W. 1982. Social organization, patterns of sexuality, and behavior of the wrasse *Coris dorsomaculata* at Miyake-jima, Japan. *Env. Biol. Fish.* 7(1): 29-38.
- Tupper, M., and W. Hunte. 1994. Recruitment dynamics of coral reef fishes in Barbados. *Mar. Ecol. Prog. Ser.* 108: 225-235.
- vanRooij, J.M., F.J. Kroon, and J.J. Videler. 1996. The social and mating system of the herbivorous reef fish *Sparisoma viride*: one-male versus multi-male groups. *Env. Biol. Fish.* 47: 353-378.
- Victor, B.C. 1986. Larval settlement and juvenile mortality in a recruitment-limited coral reef fish population. *Ecol. Monogr.* 56: 145-160.
- Wahl, C.M., E.L. Mills, W.N. McFarland, and J.S. Degisi. 1993. Ontogenetic changes in prey selection and visual acuity of the yellow perch, *Perca flavescens*. *Can. J. Fish. Aquat. Sci.* 50(4): 743-749.
- Wainwright, P.C. 1988. Morphology and ecology: functional basis of feeding constraints in Caribbean labrid fishes. *Ecology* 69 (3): 635-645.

- Waldner, R.E. and D.R. Robertson. 1980. Patterns of habitat partitioning by eight species of territorial Caribbean damselfishes (Pisces: Pomacentridae). *Bull. Mar. Sci.* 30: 171-186.
- Walsh, W.J. 1987. Patterns of recruitment and spawning in Hawaiian reef fishes. *Env. Biol. Fish.* 18:257-276.
- Wanzenboeck, J., M. Zaunreiter, C.M. Wahl, and D.L.G. Noakes. 1996. Comparison of behavioural and morphological measures of visual resolution during ontogeny of roach (*Rutilus rutilus*) and yellow perch (*Perca flavescens*). *Can. J. Fish. Aquat. Sci.* 53(7): 1506-1512.
- Warden, R.L. Jr, and W.J. Lorio. 1975. Movements of largemouth bass (*Micropterus salmoides*) in impounded waters as determined by underwater telemetry. *Trans. Am. Fish. Soc.* 104: 696-702.
- Warner, R.R. 1975. Adaptive significance of sequential hermaphroditism in animals. *Am. Nat.* 109: 61-82.
- Warner, R.R. 1995. Large mating aggregations and daily long-distance spawning migrations in the bluehead wrasse, *Thalassoma bifasciatum*. *Env. Biol. Fish.* 44:337-345.
- Warner, R.R. and S.G. Hoffman. 1980a. Local population size as a determinant of mating system and sexual composition in two tropical marine fishes (*Thalassoma* sp.) *Evolution.* 34(3): 508-518.
- Warner, R.R., and S.G. Hoffman. 1980b. Population density and the economics of territorial defense in a coral reef fish. *Ecology.* 61(4): 772-780.
- Warner, R.R., and D.R. Robertson. 1978. Sexual Patterns in the Labroid Fishes of the Western Caribbean, I: The wrasses (Labridae). *Smithsonian Contributions to Zoology.* 254.
- Warner, R.R., D.R. Robertson, and E.G. Leigh, Jr. 1975. Sex change and sexual selection: The reproductive biology of a labrid fish is used to illuminate a theory of sex change. *Science.* 190: 633-638.
- Wauters, L., and A.A. Dhondt. 1992. Spacing behavior of red squirrels, *Sciurus vulgaris*: variation between habitats and the sexes. *Anim. Behav.* 43: 297-311.
- Wauters, L.A., and J. Gurnell. 1999. The mechanism of replacement of red squirrels by grey squirrels: a test of the interference competition hypothesis. *Ethology.* 105: 1053-1071.
- Wellington, G. M. 1992. Habitat selection and juvenile persistence control the distribution of two closely related Caribbean damselfishes. *Oecologia* 90:500-508.
- Wennhage, H., and L. Pihl. 1994. Substratum selection by juvenile plaice (*Pleuronectes platessa* L.): impact of benthic microalgae and filamentous macroalgae. *Netherlands J. of Sea Research.* 32: 343-351.

- Werner, E.E., and J.F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. *Ann. Rev. Ecol. Syst.* 15: 393-425.
- Werner, E.E., J.F. Gilliam, D.J. Hall, and G.G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology*. 64(6): 1540-1548.
- White, G.C., and R.A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, California.
- Williams, D.McB. 1980. Dynamics of the pomacentrid community on small patch reefs in One Tree Lagoon (Great Barrier Reef). *Bull. Mar. Sci.* 30: 159-170.
- Williams, D.McB., and A.I. Hatcher. 1983. Structure of fish communities on outer sloped of inshore, mid-shelf and outer shelf reefs of the Great Barrier Reef. *Mar. Ecol. Prog. Ser.* 10: 239-250.
- Williams, D.McB., and P.F. Sale. 1981. Spatial and temporal patterns of recruitment of juvenile coral reef fishes to coral habitats within 'One Tree Lagoon', Great Barrier Reef. *Mar. Biol.* 65: 245-253.
- Wilson, S.F., D.M. Shackleton, and K.L. Campbell. 1998. Making habitat-availability estimates spatially explicit. *Wildlife Soc. Bull.* 26(3): 626-631.
- Winfield, I.J. 1991. Fishes, waterfowl, and eutrophied ecosystems: a perspective from a European vertebrate ecologist. *Mem. Ist. Ital. Idrobiol.* 48: 113-126.
- Wissinger, S.A. 1992. Niche overlap and the potential for competition and intraguild predation between size-structured populations. *Ecology*. 73(4): 1431-1444.
- Wootton, R.J. 1990. Ecology of teleost fishes. London: Chapman and Hall.
- Worton, B.J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*. 70(1): 164-168.
- Wu, L. and D.A. Culver. 1992. Ontogenetic diet shift in Lake Erie age-0 yellow perch (*Perca flavescens*): A size-related response to zooplankton density. *Can. J. Fish. Aquat. Sci.* 49 (9): 1932-1937.
- Zar, J.H. 1996. Biostatistical Analysis. 3rd Edition. Prentice Hall. New Jersey.
- Zeller, D.C. 1997. Home range and activity patterns of the coral trout *Plectropomus leopardus* (Serranidae). *Mar. Ecol. Prog. Ser.* 154: 65-77.

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